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Family Pachastrellidae Carter, 1875

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Pachastrellidae Carter (Demospongiae: Astrophorida), including Theneidae Carter, contains 12 valid genera and 2 subgenera. Most genera contain cup-like, massive, and submassive species and are distributed from tropical to high latitudes, mostly in epibathyal and bathyal habitats. A few genera also include encrusting or cavity-filling forms found predominantly in tropical or temperate shallow-water habitats. This astrophorid family is defined by the possession of tetraxons (calthrops, short-shafted triaenes, mesotriaene-derived desmas, or long-shafted triaenes) in combination with streptasters (never euasters) and in most cases by monaxonic microscleres (i.e., microxeas, microstyles and microstrongyles). The microscleres are densely packed at the ectosome forming a feltwork. The relationship between genera possessing a typical pachastrellid skeleton and some genera bearing tetraxial desmas other than mesotriaene-derived desmas (mesotriders), which have traditional been included in Lithistida, is still a matter of contention.
Keywords: Porifera; Demospongiae; Astrophorida; Pachastrellidae; *Acanthotriaena*; *Ancorella*; *Brachiaster*; *Characella*; *Cladothenea*; *Dercitus*; *Pachastrella*; *Poecillastra*; *Stoeba*; *Thenea*; *Triptolemma*; *Vulcanella*; *Vulcanella (Annulastrella)* subgen.nov., *Vulcanella (Vulcanella)*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Pachastrellidae Carter, 1875c. Theneidae Carter, 1883b. Streptastrosa Sollas, 1888. [Asterostreptidae] Topsent, 1902. [Astrostreptidae] Auct. (*lapsus*). Metastrosa Lendenfeld, 1906. Halinidae de Laubenfels, 1934.

Definition

Astrophorida having a variety of tetraxons (i.e., calthrops, short-shafted triaenes, mesotriaene, mesotriaene-derived desmas, or long-shafted triaenes) in combination with streptasters (never euasters) and, in most cases, monaxonic microscleres (usually microxeas and/or microstrongyles).

Diagnosis

Astrophorida whose megascleres are calthrops, short-shafted triaenes, mesotrider desmas, or long-shafted triaenes (Fig. 1), usually, but not always, in combination with monaxonic megascleres (typically oxeas, rarely styles or strongyles). Microscleres are streptasters and/or monaxonic microscleres (Fig. 2), but never euasters. The ectosomal skeleton is constituted by a layer of microscleres, forming a feltwork that has occassionally been referred to as "pseudocortex".

Scope

Prior to this review, Pachastrellidae and Theneidae were considered to be separate and valid families (e.g., Lévi, 1973). Theneidae was diagnosed as having special aquiferous openings, long-shafted triaenes and metasters, while Pachastrellidae was defined as having calthrop-like tetraxons and a large variety of streptasters. However, it has been shown that: (1) several species of typical pachastrellid genera (such as *Characella*, *Poecillastra* and *Vulcanella* (=*Sphinctrella*)) have long-shafted triaenes; (2) *Vulcanella* species also have special aquiferous openings (Fig. 3D–E); and (3) a wide variety of streptasters, apart from metasters, can be found in many species traditionally allocated to both Theneidae and Pachastrellidae. Pachastrellidae and Theneidae also shared the absence of euasters.

Given that skeletal characters do not allow inequivocal discrimination between Theneidae and Pachastrellidae, both families are formally merged here. This proposal is not a new one, as it has been previously suggested by several earlier authors. Sollas (1888) suggested the name Streptastrosa (with Demus level) for a general astrophorid line including Pachastrellidae and Theneidae, and characterized by the presence of streptasters in combination with tetraxons. Sollas also stated (1888: CIV): "indeed, there is a most evident transition from *Thenea* to *Pachastrella* through the intermediate genus *Poecillastra*". The Sollas 'Demus' taxon was also used by Lendenfeld (1906) and Lebwohl (1914), but under the name Metastrosa. Combining the families was first proposed by Topsent (1902), who maintained Theneidae and Pachastrellidae as subfamilies of his new family [Asterostreptidae] (which is a *nomen nudum* because there is no genus *Asterostrepta*, *-us*). Ferrer-Hernández (1914b) and Wilson (1925) also supported this combination but did not differentiate the subfamilies. The former author proposed the name Pachastrellidae while the latter erroneously considered that Theneidae had priority over Pachastrellidae. More recently, the combined family, under the name Pachastrellidae, was also claimed by Wiedenmayer (1994).

Twelve nominal genera are considered here to be valid within Pachastrellidae: *Acanthotriaena* Vacelet, Vasseur & Lévi, 1976; *Ancorella* Lendenfeld, 1906; *Brachiaster* Wilson, 1925; *Characella* Sollas, 1886a; *Cladothenea* Koltun, 1964b; *Dercitus* Gray, 1867a; *Pachastrella* Schmidt, 1868; *Poecillastra* Sollas, 1888; *Stoeba* Sollas, 1888; *Thenea* Gray, 1867a; *Triptolemma* de Laubenfels, 1955b; *Vulcanella* Sollas, 1886a.

Several other nominal genera previously assigned to Pachastrellidae (including Theneidae) are herein abandoned, synonymised into other genera, or transferred to other families. For instance, *Dercitancorina* Topsent, 1902, formerly erected for *Pachastrella lesinensis* Lendenfeld, 1894, is now regarded as a junior synonym of *Stoeba*, being *S. lesinensis* a valid species.

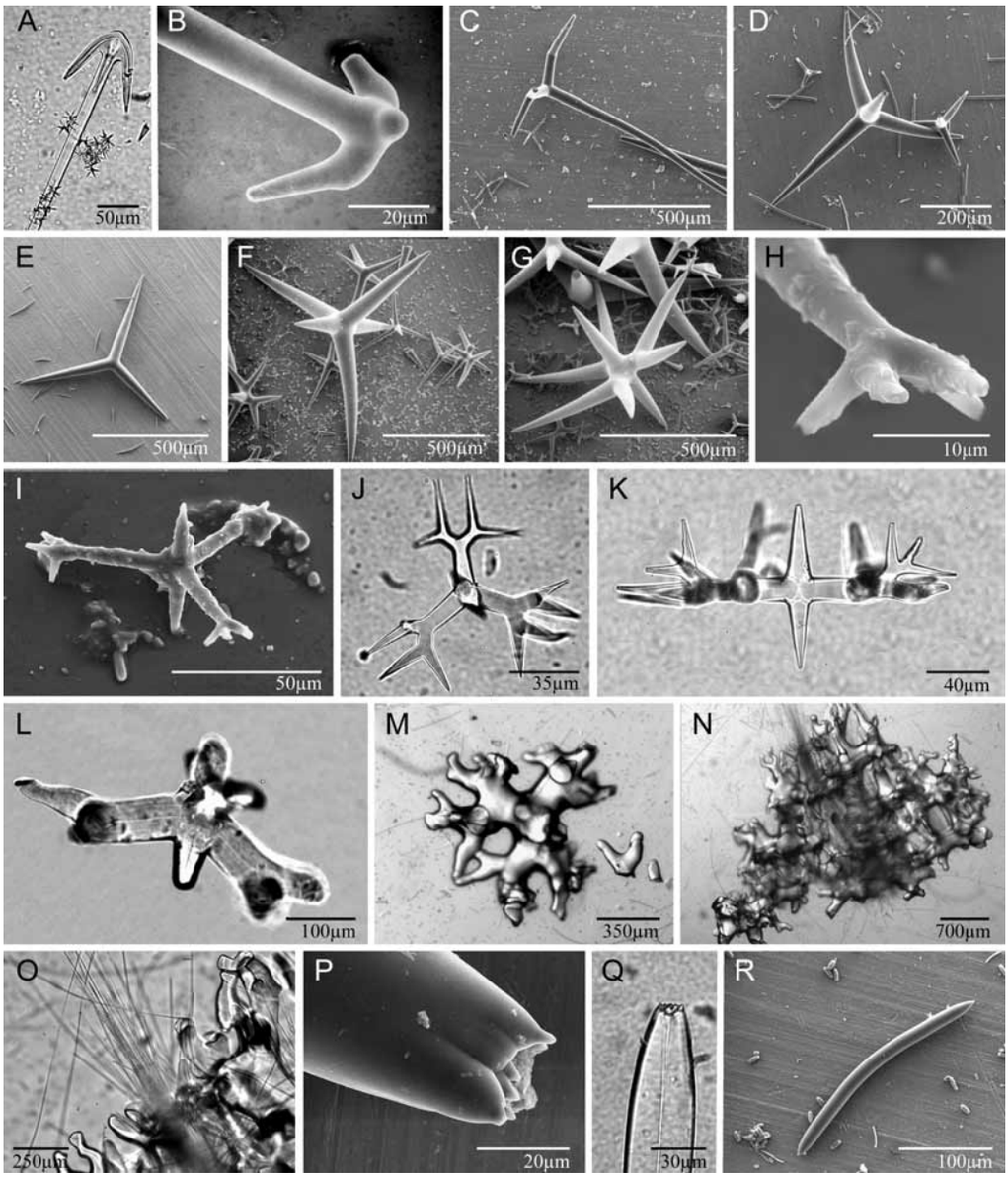

Fig. 1. Pachastrellidae megascleres. A, anatriaene of *Thenea*. B, anatriaene of *Characella*. C, dichotriaene of *Cladothenea*. D, regular calthrops and hastate oxeas of *Pachastrella*. E, triactinal tetraxon of *Characella*. F–G, mesocalthrop and mesodichotriaene, respectively, of an undescribed *Pachastrella* from the Galapagos Islands. H–I, end of multibranched clad in mesotriaene of *Triptolemma* and the entire spicule, respectively. J–M, several branching stages of mesotriaenes in transition to mesotrider desmas in *Brachiaster*. N–O, general view and detail of a piece of the choanosomal network made by fused mesotriders and pierced by fascicles of strongyloxeas in *Brachiaster*. P–Q, details of the end of cladotyles in *Cladothenea*. R, hastate oxea of *Pachastrella*.

Pachamphilla Lendenfeld, 1906 (type species *P. alata* Lendenfeld, 1906) is a junior synonym of the ancorinid genus *Penares* Gray, 1867a (see also Lévi, 1967b). The monotypic genus *Chelotropaena* Lendenfeld, 1906, with type species *C. tenuirhabda* Lendenfeld, 1906, is a synonym of *Poecillastra.* The genus *Yodomia* Lebwohl, 1914, with type species *Y. ijimai* Lebwohl, 1914, is a synonym of *Characella*, with its other known nominal species – *Y. perfecta* Dendy, 1916c – being a *Pachastrella* species. The genus *Halinastra* de Laubenfels, 1936a, formerly erected for *Pachastrella exostotica* Schmidt, 1868, is herein considered to be a junior synomyn of *Stoeba*, with *S. exostotica* a valid species.

Several other genera had previously been discarded for different reasons. For instance, the genus *Papyrula* Schmidt, 1868, which was formerly considered as a theneid (e.g., Lendenfeld, 1906), is now regarded as a junior synonym of the ancorinid genus *Penares* (see chapter on Ancorinidae). The genus *Plakinastrella* Schulze, 1880, which was included (as *Placinastrella*) in Theneidade by Sollas (1888) and in Pachastrellidae by Lendenfeld (1894), is now regarded as a valid plakinid genus (see chapter on Plakinidae). The genus *Nethea* Sollas, 1888 was invalidated following Lévi (1973) and Maldonado (1993), as it was an artificial taxon erected to contain species whose tetraxons have underdeveloped actines; its type species *Nethea nana* (Carter, 1880a) and another species *N. amygdaloides* (Carter, 1876) clearly belong to *Poecillastra*, while *Nethea dissimilis* Sarà, 1959a probably belongs to the genus *Stoeba*. The genera *Calthropella* Sollas, 1888 and

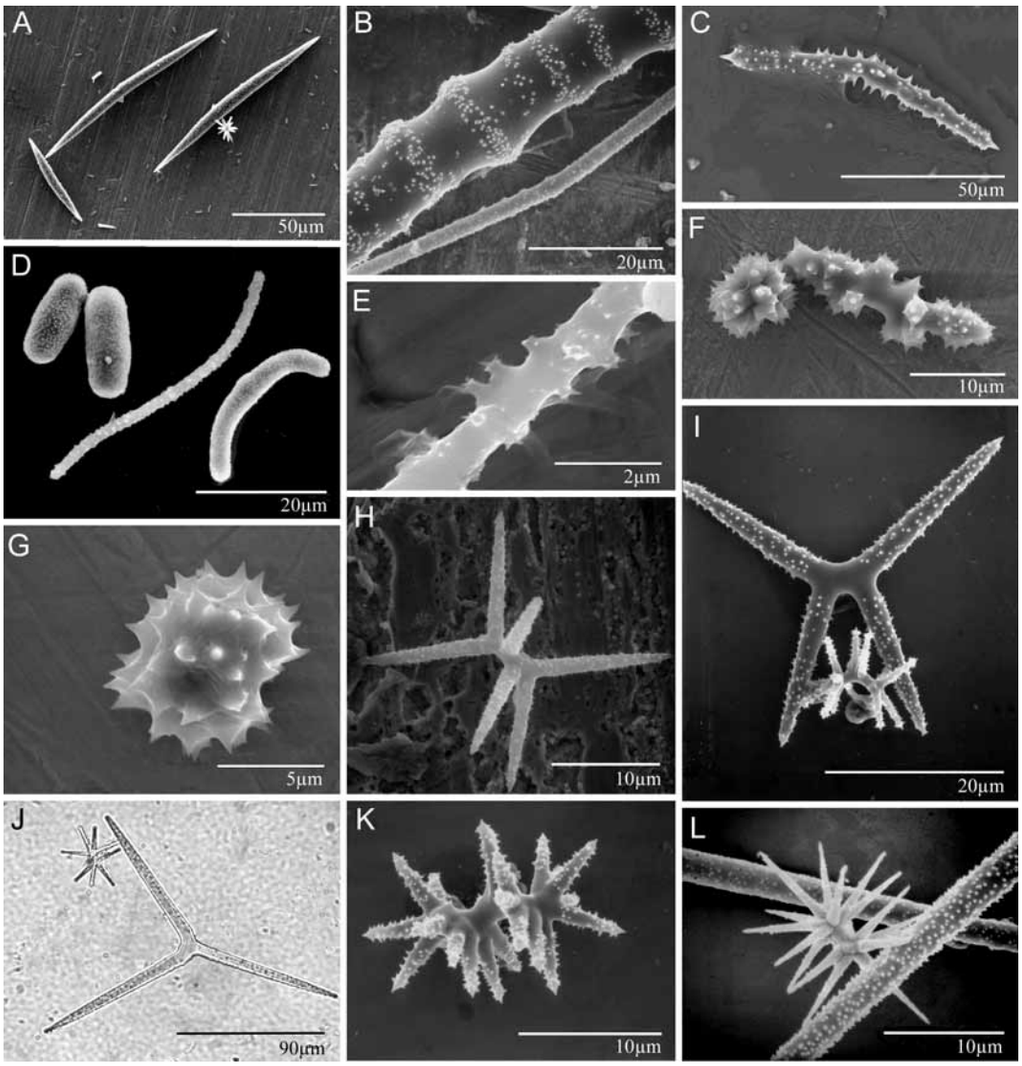

Fig. 2. Pachastrellidae microscleres. A, large and small, spiny microxeas of *Characella*. B, large annulate microxea and small, uniformly spiny microxea of *Vulcanella*. C, microxea of *Triptolemma*. D, oval microstrongyles, spiraster-like microstrongyles and curved, oval microstrongyles of *Pachastrella*. E, detail of ornamentation of spiraster-like microstrongyle, suggesting that this spicule type is a streptaster with reduced actines. F, sanidasters of *Stoeba*. G, detail of a sanidaster-ataxaster of *Stoeba*, showing a spheraster-like morphology, likely derived from an evolutionary shortening of the central axis. H, metaster of *Pachastrella*. I, large plesiaster and small spiraster of *Poecillastra*. J, large plesiaster and small amphiaster of *Cladothenea*. K, spiraster of *Vulcanella*. L, amphiaster of *Characella* on two large, spiny microxeas.

[*Corticella*] Sollas, 1888, (preocc. by *Corticella* Ehrenberg, 1872, Protoctista), regarded as pachastrellids by Sollas (1888) and Lendenfeld (1894) respectively, are now considered to be synonyms, with the senior genus *Calthropella* being the type of the family Calthropellidae (see chapter on Calthropellidae). Similarly, the genus *Pachastrissa* Lendenfeld, 1903, formerly erected in Pachastrellidae, is currently considered a valid genus of Calthropellidae. The monotypic genus *Neothenea* de Laubenfels, 1934 was invalidated by Van Soest & Stentoft (1988), who confirmed that the type species, *Neothenea enae* de Laubenfels, 1934, was likely conspecific with *Characella aspera* Sollas, 1886a (the type species of *Characella*). Finally, the name [*Picraster*] attributed to Sollas (1888) by de Laubenfels (1936a) for a putative pachastrellid is apparently an error, as no data has been found in the literature to validate de Laubenfels' information (i.e., *nomen dubium*).

Undoubtedly the present scope of Pachastrellidae, as defined here, will change on the basis of future genetic, biochemical, and anatomical findings, being difficult to predict the direction of such changes. Future research might result in a family split, reinstating the former theneids and pachastrellids, as suggested by an anonymous reviewer. However, it is more likely that the present family concept will be expanded by the addition of a variety of genera from the polyphyletic 'order Lithistida', which is gradually being dismembered. Indeed, a potential relationship between 'lithistids' and pachastrellids was suggested by some earlier workers, such as Carter (1875c), who even included several 'lithistids' in his family Pachastrellidae. This relationship between pachastrellids and desma-bearing genera also appears to be supported by the Late-Cretaceous genus *Propachastrella* Schrammen, 1910 (type species *Pachastrella primaeva* Zittel, 1878b †), which is characterized by calthrop-like spicules with irregularly curved actines ended in syzygial plates, showing a morphology transitional between regular calthrops and tetraxonic desmas (e.g., Wiedenmayer, 1994). The affinity between Pachastrellidae and some 'lithistid' genera is

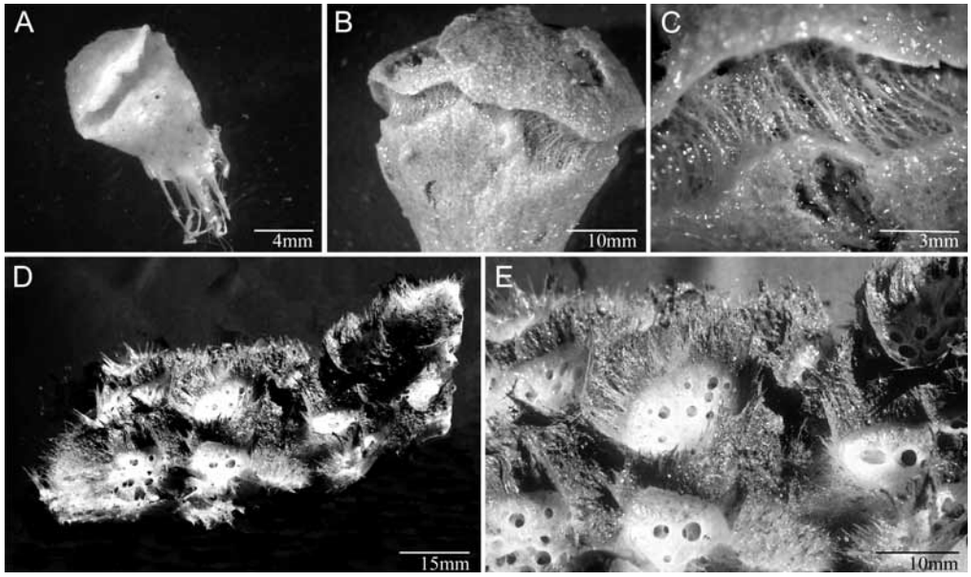

Fig. 3. Pachastrellids with specialized aquiferous systems. A–C, *Thenea muricata*. A, specimen showing basal roots and a transversal recess of the body, in which the inhalant areas are located. B–C, details of the inhalant areas and ostioles. D–E, *Vulcanella tricornis*. D, specimen showing the atrial areas of the exhalant side. E, detail of the exhalant areas, which are surrounded by a largely protruding palisade of flexuous spicules.

also supported by the spiny tetraxons of *Acanthotriaena* and the multibranched mesotriaenes of *Triptolemma* and *Brachiaster*, which even become tetraxonic desmas (mesotriders) in this latter genus. The stout, short-shafted dichotriaenes of some species of the genus *Stoeba* also resemble the tetraxons of some 'lithistids'. On the basis of morphological similarities some authors (e.g., Reid, 1970) have suggested the hypothesis of a common ancestor for streptaster-bearing 'lithistids' and pachastrellids. Indeed, the idea that a variety of tetraxon-bearing 'lithistids' may be pachastrellids should be kept in mind when reallocating some of the genera currently in the 'order Lithistida'.

The diagnoses and definitions of genera revised here are expanded to include both the traits of the type species and the most distinctive traits that consistently occur in all or most species in each genus. Lists of all valid species in each genus are not provided although special attention has been given to the remarks on each genus to clarify the taxonomic status of controversial species assigned to them.

KEY TO GENERA

(1) Tetraxons being only a variety of long-shafted forms (i.e., triaenes) 2
Tetraxons being calthrops/short-shafted tetraxons alone or in combination with long-shafted forms 3
(2) With cladotyles (styles with a crown of tubercles at its rounded end) ..... ***Cladothenea***
Without cladotylotes; monaxonic megascleres being regular oxeas or styles ..... ***Thenea***
(3) With a number of short-shafted tetraxons becoming mesotriaena-derived desmas (mesotriders) ..... ***Brachiaster***
Tetraxons never becoming mesotrider desmas 4
(4) Tetraxons with spiny rhabdome ..... ***Acanthotriaena***
Tetraxons being entirely smooth 5
(5) All tetraxons being pentactinal (i.e., mesotriaenes) ..... ***Triptolemma***
Tetraxons being triactinal and tetractinal forms, alone or in combination with mesotriaenes 6
(6) Without streptasters ..... ***Ancorella***
With streptasters 7
(7) Without microxeas 8
With microxeas 10
(8) With toxa ..... ***Dercitus***
Without toxa 9
(9) With oval microstrongyles ..... ***Pachastrella***
Without oval microstrongyles; with microrhabd-like sanidasters ..... ***Stoeba***
(10) Cribiporal oscules surrounded by a palisade of protruding spicules; annulate microxeas and/or annulate plesiasters ..... ***Vulcanella***
Simple oscules; uniformly spiny microxeas or, more rarely, smooth microxeas 11
(11) Microxeas in at least two categories; streptasters never being plesiasters ..... ***Characella***
Microxeas in one category; streptasters always including plesiasters ..... ***Poecillastra***

ACANTHOTRIAENA VACELET, VASSEUR & LÉVI, 1976

Synonymy

Acanthotriaena Vacelet, Vasseur & Lévi, 1976: 21.

Type species

Acanthotriaena crypta Vacelet, Vasseur & Lévi, 1976: 21 (by monotypy).

Definition

Pachastrellidae having megascleres of which are triaenes with spiny rhabdomes (acanthotriaenes).

Diagnosis

Encrusting Pachastrellidae, the megascleres of which are spiny tetraxons (acanthotriaenes) and small oxeas; its microscleres are spirasters and raphides.

Remarks

The family allocation for *Acanthotriaena,* a monotypic genus known only by fragments of its type species, is arguable. This genus is apparently related to other genera with spiny tetraxons, such as the Jurassic-Cretaceous *Acanthastrella* Schrammen, 1924a and the Recent *Thrombus* Sollas, 1888. Furthermore, the skeleton of two species of the latter genus, *Thrombus abyssi* (Carter, 1873b) and *Thrombus jancai* Lehnert, 1998, consists of a combination of spiny short-shafted tetraxons and peculiar amphiasters. Based on their skeletal similarities it is possible that *Acanthotriaena* is not a pachastrellid but a second member of the unconnected, monotypic family *Thrombidae*. Conversely, it is also possible that *Thrombus* is a reduced pachastrellid and thus Thrombidae an empty family (see chapter on Thrombidae for alternative views). Dichotriaenes and anatriaenes with acanthose decoration on clads and rhabdome have also been reported in the late-Triassic genus *Costamorpha* Mostler, 1986 (see also Wiedenmayer, 1994).

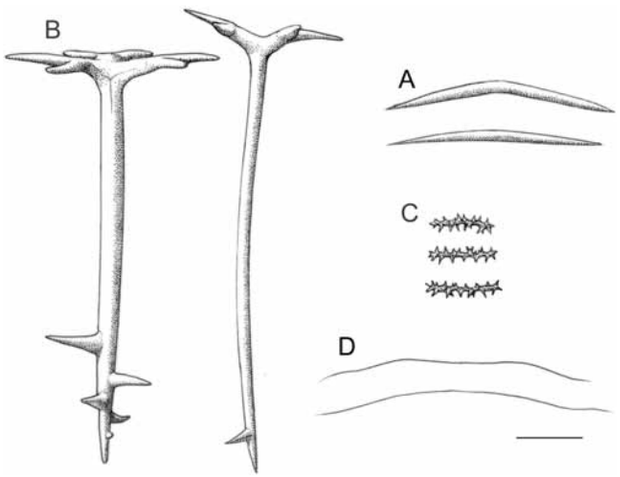

Fig. 4. *Acanthotriaena*. *A. crypta*, holotype. A, smooth oxeas (scale 35 μm). B, acanthodichotriaenes (scale 75 μm). C, spirasters (scale 17 μm). D, flexuous raphides (scale 40 μm).

Description of type species

Acanthotriaena crypta Vacelet, Vasseur & Lévi, 1976 (Fig. 4).

Material examined. None. The description is taken from Vacelet *et al*. (1976).

Description. Small encrusting sponge filling cavities on the underside of a boulder, from which only small fragments could be collected. The material did not allow description of the skeletal structure and casts doubts about the exogenous or endogenous origin for some of the spicule types found. The skeleton consists of four spicule types: oxeas, acanthotriaenes, spirasters and raphides. Oxeas are smooth, regular in shape, curved at the middle, and measuring 115–130 × 5–6 μm. Acanthotriaenes are dichotriaenes with smooth protoclads and deuteroclads measuring 15–35 μm × 5–15 μm and 15–55 × 5–15 μm, respectively, and a spiny rhabdome measuring 155–500 × 5–20 μm. The rhabdome, although it may occasionally be smooth, is often provided with 1–6 conical spines, each 40 μm long, that contain a branch of axial canal in their bases. Spirasters have short actines relative to the central axis and measure 16–18 × 1 μm in total length. Raphides are flexuous and measure 50–250 × 0.5–1 μm.

Remarks. The genus and species is known only from the holotype. Although the oxeas described above were intimately intermingled with the remaining spicules, Vacelet *et al*. (1976) suggested the possibility that they may actually belong to a *Cliona*.

ANCORELLA LENDENFELD, 1906

Synonymy

Ancorella Lendenfeld, 1906: 248.

Type species

Ancorella paulini Lendenfeld, 1906: 248 (by monotypy).

Definition

Pachastrellidae without streptasters.

Diagnosis

Pachastrellidae without streptasters. Megascleres are strongyloxeas transitional to strongyles, calthrops reduced to three actines, and anatriaenes. Microscleres are uniformly and finely spiny microxeas.

Remarks

The absence of asters complicate the taxonomic interpretation of this monotypic genus. Although *Ancorella* has been traditionally considered as a pachastrellid that has lost its streptasters (Lendenfeld, 1906), it might also be regarded as an ancorinid that had lost its euasters. However, several of its features, which also occur in typical pachastrellid genera, suggest that *Ancorella* is a skeletally-reduced pachastrellid, as follows: the general appearance and consistence of the sponge, the ectosomal feltwork of microxeas, the arrangement,

shape and size of the reductional stages of calthrops, the presence of anatriaenes with a blunt rhabdome (see Maldonado 1996), and the decoration of the microxeas. Indeed, the body form and skeletal features of the type species, *Ancorella paulini* Lendenfeld, 1906, strongly resemble those of the Atlantic-Mediterranean *Characella tripodaria* (Schmidt, 1868), which is characterized by the presence of anatriaenes with blunt rhabdomes and malformed clads (Figs 1B, 7M), as well as malformed and reduced calthrops, and, what is more important, an extremely low density of streptasters in its tissue (Maldonado, 1996).

Description of type species

Ancorella paulini Lendenfeld, 1906 (Fig. 5).

Material examined. Holotype: BMNH 1908.2.9.199–122 (slides).

Description. Two specimens collected. One specimen is a triangular, plate-like sponge, 75 mm long, 55 mm wide and 30 mm thick, attached to the substratum through one of the sides. The other is a 115 mm long encrustation growing on a coral. Subspherical protuberances give a lumpy, sulcate appearance to the surface. Aquiferous orifices are not visible on the sponge surface, but abundant aquiferous canals, up to 5 mm wide, occur in the choanosome. Color in alcohol is light brown (from Lendenfeld, 1906). Spicules consist of strongyles transitional to strongyloxeas, triactinal and diactinal spicules derived from calthrops and short-shafted triaenes, anatriaenes and microxeas in a single size category. Strongyloxeas transitional to strongyles are slightly curved, centrotylote, measuring 1300–2300 × 18–26 μm. Triactinal and diactinal spicules are likely derived from calthrops and have straight, slender actines measuring 200–990 × 20–70 μm and 600–1100 × 40–70 μm, respectively. Anatriaenes have blunt rhabdomes and frequent malformations in the clads; sometimes the whole cladome is reduced to a knob, yielding a spicule morphology similar to that of a tylostyle; clads measure 45–60 μm in length and rhabdomes measure 750–1100 × 5–11 μm. Microxeas are in a single size category (67.5–210 × 2.5–4 μm), being slightly curved, uniformly and finely spiny, and with acerate to hastate points. The ectosomal skeleton consists of a feltwork of microxeas. It is internally reinforced by abundant reduced calthrops and few strongyloxeas, both placed tangentially to the sponge surface. Anatriaenes, arranged perpendicular to the surface, pierce the ectosome projecting the cladome out of the sponge. Microxeas, strongyloxeas and calthrop-derived spicules also occur abundantly in the choanosome.

Remarks. A category of smooth microxeas mentioned in the original description and omitted herein is likely to be exogenous to the sponge, as also suggested by Lendenfeld (1906). The type species is known only from type material collected off the Pacific coast of Chile (38°34′S, 77°38′66″W) at 672 m depth.

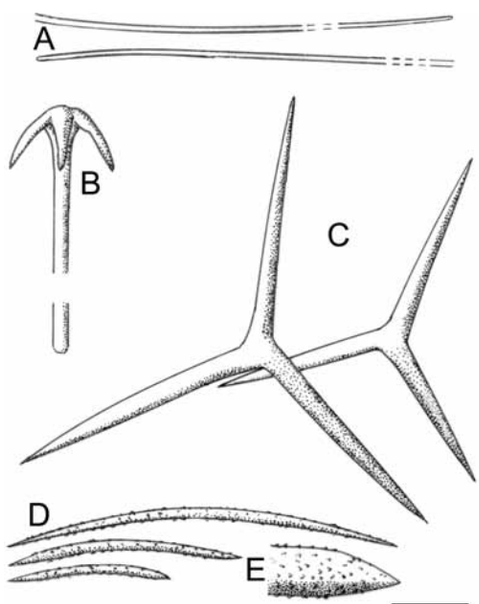

Fig. 5. *Ancorella. A. paulini*, holotype. A, fragments of long strongyloxeas (scale 250 μm). B, anatriaene with blunt rhabdomes (scale 50 μm). C, triactinal tetraxons (scale 250 μm). D, spiny microxeas (scale 40 μm). E, detail of microxea end (scale 6 μm).

BRACHIASTER WILSON, 1925

Synonymy

Brachiaster Wilson, 1925: 471.

Type species

Brachiaster simplex Wilson, 1925: 471 (by monotypy).

Definition

Pachastrellidae, whose tetraxons are short-shafted triaenes and/or mesotriaenes that become mesotrider desmas.

Diagnosis

Megascleres are styloxeas, hastate oxeas, short-shafted triaenes and mesotriaenes with clads diversely branched transitional to tetracrepidal and mesotrider desmas, respectively. Desmas can be articulated through subcircular syzygial plates, but, at the innermost parts of the sponge, they fuse to each other, making a solid network. Microscleres are spiny microxeas, oval microstrongyles, and amphiasters transitional to metasters.

Remarks

The diagnosis of this monotypic genus given above is based on the skeletal traits reported from the two available records of its type species (Wilson, 1925; Lévi & Lévi, 1989). Nevertheless, the skeletal differences between the material collected in both cases suggests the existence of high levels of intraspecific skeletal variability and the possibility of further diagnosis readjustments when additional material is collected.

Description of type species

Brachiaster simplex Wilson, 1925 (Figs 1J–O, 6).

Material examined. Holotype (not seen): USNM. Specimen of Lévi & Lévi (1989): MNHN.

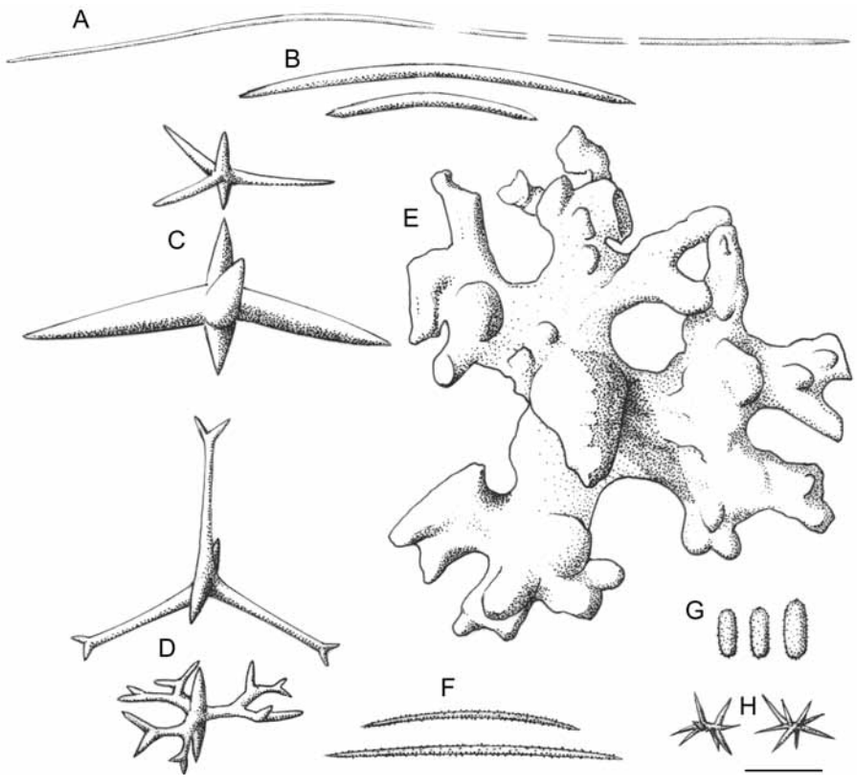

Fig. 6. *Brachiaster. B. simplex*. A, styloxea (scale 150 μm). B, hastate oxeas (scale 40 μm). C, short-shafted mesotriaenes with undivided clads (scale 75 μm). D, short-shafted mesotriaenes with diversely branched clads (scale 75 μm). E, desma mesotrider (scale 200 μm). F, spiny microxeas (scale 40 μm). G, oval microstrongyles(scale 20 μm). H, amphiasters transitional to metasters (scale 20 μm).

Description. Cup-like sponge, 145 mm tall, 120 mm wide and with a 25 mm thick body wall. Color is grayish ochre with pinkish tones. Two different regions are externally distinguished on the concave side of the sponge: a central region, where the surface is rugose and hispid, and a peripheral region, where the surface is smooth and glabrous, with a radial striation pattern caused by the internal aquiferous canals. The spicule set in Lévi's material consists of styloxeas, hastate oxeas, a variety of mesotriaenes transitional to mesotrider desmas, microspiny microxeas, microstrongyles and streptasters. Styloxeas are long, thin, and very flexuous, measuring up to 4 mm in length and 6 mm in thickness. Hastate oxeas are smooth and slightly curved, measuring 100–225 × 6–11 μm. Mesotriaenes have nearly symmetrical rhabdomes, being clearly shorter than the clads; clads may be undivided, dichotomous, trifurcated and even multibranched. Isolated mesotriaenes, the clads of which measure 150–350 × 15–69 μm, grow irregularly in thickness and also in length to become mesotriders (300–500 × 80–250 μm), which often occur fused to each other forming a solid network. Microxeas are slightly curved, entirely and uniformly microspiny, measuring 100–160 × 3.5–5 μm. Oval microstrongyles measure 4–6 × 2–3 μm, being neither centrotylote nor curved. Streptasters, which measure 12–15 μm in total length, are a variety of amphiasters transitional to metasters, with a 4–6 μm thick axis and 4–8 μm-long actines. The skeleton of the innermost regions of the sponge body wall consists of a rigid network of mostly fused desmas, although articulate spicules can be found towards the periphery. Towards the internal side of the cup, the desma layer is externally covered by a region of isolated mesotriaenes, which in turn is externally covered by a feltwork of oval microstrongyles. Fascicles of styles and styloxeas, passing through the holes of the desma network, run from the innermost choanosome to the internal side of the sponge, which is slightly hispid. Towards the external side of the cup, the internal layer of desmas is covered by an outermost layer rich in cells, oval microstrongyles and metasters. Microxeas are scattered in the interstitial tissue.

Remarks. The description above is based on Wilson's (1925) initial description and re-examination of Lévi & Lévi's (1989) subsequent material. By comparing Wilson's and Lévi's descriptions it appears that the presence or absence of dichotriaenes is a subject of intraspecific variability. Dichotriaenes were reported by Wilson (1925) in addition to the mesotriaenes, both types becoming desmas. Nevertheless, both observations are compatible as it is likely that the mesotriaenes may grow initially through a dichotriaene stage before developing the epirhabdome.

The type species is known from Philippine waters at 198–188 m depth (Wilson, 1925; Lévi & Lévi, 1989).

CHARACELLA SOLLAS, 1886

Synonymy

Characella Sollas, 1886a: 186. *Yodomia* Lebwohl, 1914. *Neothenea* de Laubenfels, 1934.

Type species

Characella aspera Sollas, 1886a: 186 (by original designation).

Definition

Pachastrellidae the microscleres of which consist of streptasters of straight axis (never spirasters) and at least two categories of curved monaxonic spicules (microoxea, microstyles, microstrongyloxeas).

Diagnosis

Pachastrellidae whose megascleres consist of abundant oxeas and scarce calthrops (and/or short-shafted triaenes), mostly restricted to subectosomal regions. Microscleres are spiny or smooth microxeas-microstrongyles in at least two size categories and streptasters with a straight central axis (amphiasters or sanidasters); streptasters may be very scarce in some species. Anatriaenes with cladomes that protrude the sponge surface and blunt rhabdomes embedded in the choanosome occur in some species.

Remarks

Streptasters are scattered in very low density in the tissue of several species, such as in *C. aspera* Sollas, 1888 from the North Atlantic (BMNH 1894.11.16.149–152 (slides)) and *C. tripodaria* (Schmidt, 1868) from the Atlantic-Mediterranean region (Fig. 2L; BMNH 1868.3.2.36 (slide); MNCN-36; CEAB Alb-8, Alb-31, Alb-60p). This makes *Characella* close to the monotypic genus *Ancorella* in its skeletal structure, which is characterized by the absence of streptasters and the presence of anatriaenes. It is noteworthy that anatriaenes also occur in some species of *Characella*, such as *C. tripodaria* (Fig. 1B, 7M; see also Maldonado, 1996). They were also observed in re-examination of the holotype of *C. pachastrelloides* (Carter, 1876) (BMNH 1882.7.28.125 (dry)) and in many other specimens of this species collected around Cape Saint Vincent (Fig. 7G–H) by the 'Porcupine' Expeditions (e.g., BMNH 1910.1.1.1680 (slide) Norman Coll.), as well as in specimens described by Stephens (1915a) (BMNH 1953.II.II.30) from Irish waters, and eastern-Atlantic specimens described by Lévi & Vacelet (1958). Anatriaenes have also been found in specimens of an undescribed *Characella* collected from the Galapagos Island (Maldonado & Pomponi, unpublished).

Re-examination of diverse material has also led to the conclusion that several species originally described in other astrophorid genera may belong to *Characella*. For instance, *Pachastrella connectens* Schmidt, 1870 (BMNH 1870.5.3.45 (slide), also 1870.5.3.170 (dry, fragment from type) from Florida is a valid species of *Characella* (Figs 1E, 7T–X), while *Ancorina pachastrelloides* Schmidt, 1870 (Fig. 7R–S; BMNH 1870.5.3.48 (slide)) from Florida (but not *Characella pachastrelloides* (Carter, 1876) from the northeastern Atlantic) is a junior synonym of *C. connectens* (Schmidt). Contrary to the suggestion of Topsent (1923, 1928c), *C. connectens* can be clearly distinguished from both *C. pachastrelloides* (Fig. 7G–L; BMNH 1895.1.23.2 (wet)) and all other species in the genus because the large microxeas have been replaced by strongyles. *Pachastrella stellettodes* Carter, 1885e (BMNH 1882.12.31.8 (dry)) from the Japan Sea is a valid species of *Characella*, the skeleton of which consists of oxeas, calthrops, short-shafted orthotriaenes, two size categories of microxeas, and scarce amphiasters (Figs 2A, 7N–Q). *Yodomia ijimai* Lebwohl, 1914 (BMNH 1938.7.20.4 (dry) 1938.4.20.4a (slide)), also from the Japan Sea, is also likely a junior synonym of *C. stellettodes*.

Description of type species

Characella aspera Sollas, 1886a (Fig. 7A–F).

Synonymy. *Normania goliath* Sollas, 1886a: 187.

Material examined. Holotype: BMNH 1894. 11.16.149–150 (slides).

Description. Massive sponge, with an irregular, hispid surface that shows ridges and folds. Numerous ostia are scattered on the surface, sometimes grouped in depressed areas. Oscules, 1–2 mm in diameter, are also visible on the sides and summits of the ridges. The spicule set consists of oxeas, short-shafted orthotriaenes and dichotriaenes, microxeas in two size categories, and amphiasters. Oxeas are slightly curved and fusiform, measuring 1100–2700 × 25–75 μm. Orthotriaenes have clads measuring 200–630 × 225–50 μm; dichotriaenes have protoclads and deuteroclads measuring up to 143 μm and 270 μm, respectively; rhabdomes are 200–400 × 20–45 μm in both spicule types. Microxeas are slightly curved, fusiform, smooth, never centroangulated and rarely centrotylote. There are two size categories, 50–80 × 2.5–3 μm and 150–300 × 4–5 μm, although a few microxeas of intermediate sizes occur. Amphiasters have two whorls of four to six, relatively long, thin, and sharply-pointed actines, and a relatively short and irregularly thick axis, the ends of which become sharp actines. Amphiasters measure 14–25 μm in total length along the axis and actines 18 to 23 μm. The ectosomal skeleton consists of a feltwork of microxeas supported internally by large oxeas and triaenes that pierce largely the sponge surface. The triaenes are mostly restricted to subectosomal regions and the large oxeas are irregularly scattered through the whole sponge. Microxeas are also abundant in the choanosome, particularly reinforcing the internal epithelia along with the amphiasters.

Remarks. *Characella aspera* (Fig. 7A–F), known from 640 m deep, muddy bottoms off Brazil, is clearly differentiated from the close North-Atlantic *C. pachastrelloides* (Fig. 7G–L), with the former lacking anatriaenes and spines on the microxeas. Although the holotype of *C. aspera* has short-shafted dichotriaenes in addition to the short-shafted orthotriaenes, this spicule combination should not be considered as a species specific trait. It is known that the presence/absence of dichotriaenes is subject to population variability in other species of the genus (Topsent, 1902; Maldonado, 1996). The occasional siliceous globules (40–160 μm in diameter) described in the holotype of *C. aspera* (Fig. 7F) are probably the result of failure in the silicification process and they should not be considered as a true spicule type. I also found such globules during the re-examination of the holotype of *C. stellettodes*.

CLADOTHENEA KOLTUN, 1964

Synonymy

Cladothenea Koltun, 1964b: 16.

Type species

Cladothenea andriashevi Koltun, 1964b: 16 (by monotypy).

Definition

Pachastrellidae with distinctive cladotyles, which are style-like spicules characterized by having a crown of tubercles at the rounded spicule end.

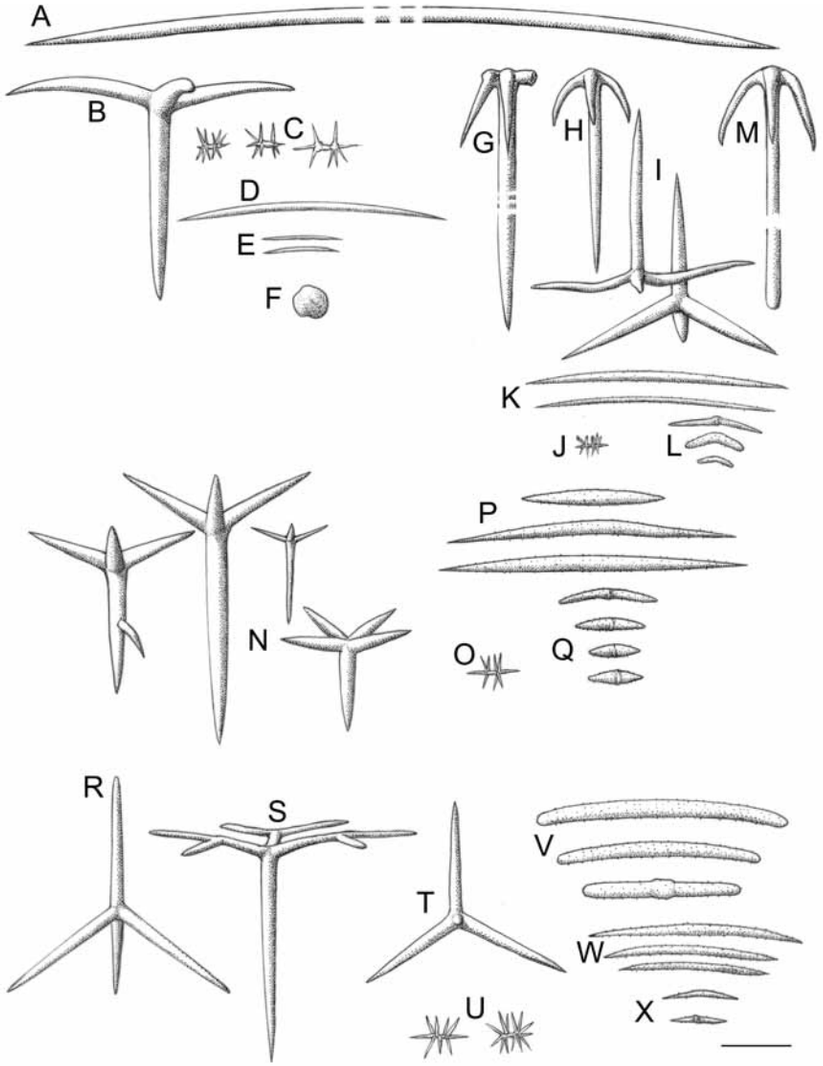

Fig. 7. *Characella*. A–F, *C. aspera*, holotype. A, oxea (scale 250 μm). B, orthotriaene (scale 150 μm). C, amphiasters (scale 25 μm). D, large microxeas (scale 80 μm). E, small microxeas (scale 80 μm). F, siliceous globule (scale 80 μm). G–L, *C. pachastrelloides*, holotype. G–H, anatriaenes (scale 100 μm). I, short-shafted orthotriaene and calthrop (scale 300 μm). J, sanidaster (scale 30 μm). K, large microxea (scale 100 μm). L, small microxea, microstrongyle-microstyle (scale 50 μm). M, *C. tripodaria*, blunt anatriaene (scale 75 μm). N–Q, *C. ijimai*, holotype. N, short-shafted plagiotriaenes, with some occasional malformations (scale 350 μm). O, amphiaster (scale 25 μm). P, large microxeas (scale 50 μm). Q, small microxeas (scale 50 μm). R–X, *C. connectens*. R–S, calthrop and dichotriaene (holotype of *Ancorina pachastrelloides* Schmidt) (scale 200 μm). T, triactinal calthrop (holotype of *Pachastrella connectens* Schmidt) (scale 200 μm). U, metasters (scale 25 μm). V, large microstrongyles (scale 80 μm). W, large microxeas (scale 80 μm). X, small microxeas (scale 50 μm).

Diagnosis

Pachastrellidae with radial, protruding fascicles of oxeas and cladotyles. Long shafted tetraxons (i.e., dichotriaenes) occur at the periphery of the choanosome, with their rhabdome pointing toward the innermost part of the pseudospherical sponge body and the cladome reinforcing the ectosomal skeleton. Microscleres are streptasters in more than one category (i.e., plesiasters and amphiasters).

Remarks

This is a monotypic pachastrellid genus characterized by the presence of cladotyles. As inferred from the spicule name, cladotyles were assumed by Koltun to be monaxons evolved from tetraxons by a process of cladome reduction. If so, such a cladome reduction may have occurred in other theneids, also leading to monaxon-like morphologies. For instance, the oxytylote – a monaxon-like spicule characterized by a terminal swelling and found in the roots of *Thenea delicata* Sollas (BMNH MC.5; 1.13)– appears to have evolved from anatriaenes (Sollas, 1888). The fact that the axial canal branches incipiently within the terminal swelling in the case of *T. delicata*, and that a canal branch goes into each tubercle in the case of *Cladothenea* (Figs 1Q, 8B), is evidence to support the tetraxon origin of this spicule. Nevertheless, it remains unexplained why the number of axial branches and tubercles ranges from 4 to 8 or even more in cladotyles. Note that Koltun's (1964b) concept of a cladotyle differs from that of Boury-Esnault & Rützler (1997), in which they are considered to be spicules with a cladome at one end and a tyle at the other. Cladotyle-like spicules, called cladotylostyles, also occur in the

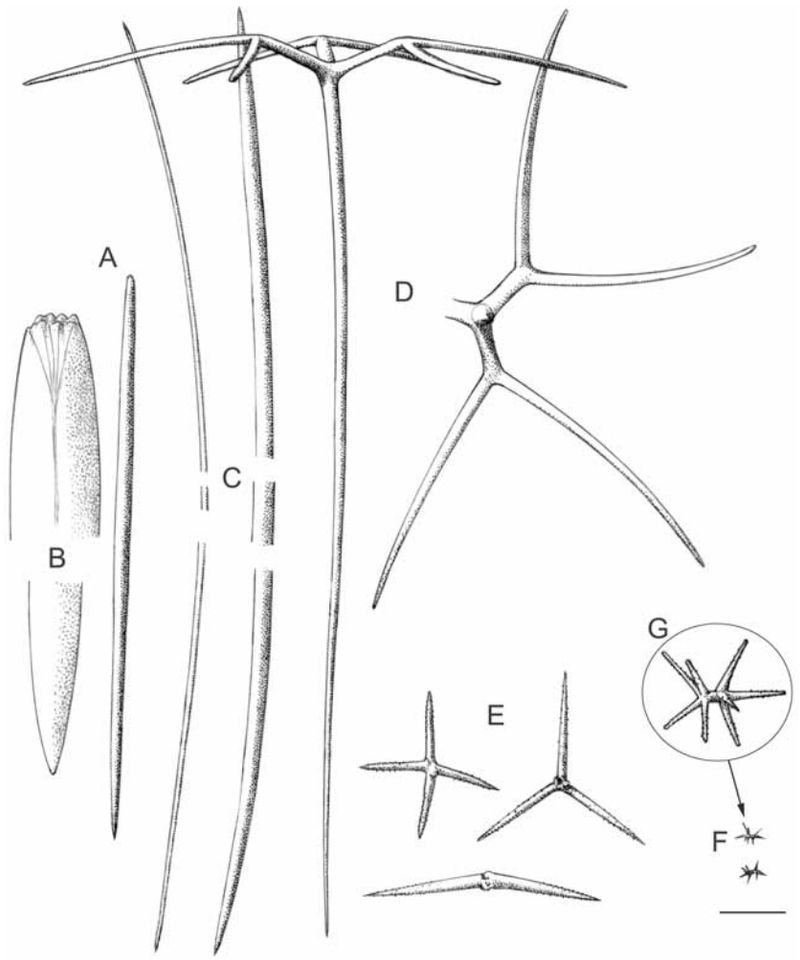

Fig. 8. *Cladothenea. C. andriashevi*, holotype. A, cladotyles (scale 40 μm). B, cladotyle ends in detail, showing axial canals (scale 200 μm). C, oxeas (scale 200 μm). D, dichotriaene and detail of dichotriaene clads (scale 200 μm). E, tetractinal, triactinal, and diactinal plesiasters (scale 70 μm). F, amphiasters (scale 70 μm). G, detail of amphiaster (scale 10 μm).

hadromerid genera *Tylexocladus* Topsent, 1898b and *Sphaerotylus* Topsent, 1898b, which are apparently unrelated to pachastrellidae.

The resemblance in skeletal structure and external morphology between *Cladothenea* and *Thenea* is striking, the two only differentiated significantly by the presence or absence of a poorly understood spicule, the cladotyle. This, along with the fact that *Cladothenea* is a monotypic genus and known only from a single, fragmented individual, suggests further re-assessment of the genus if additional material comes to hand.

Description of type species

Cladothenea andriashevi Koltun, 1964b (Figs 1C, 1P–Q, 2J, 8).

Material examined. Holotype: ZIL 6300 (skeletal slides).

Description. Holotype fragmented in several, 5–10 mm pieces, precluding a proper description of the external sponge morphology. Sponge originally described as a gray, apparently subspherical individual, with a deep transverse furrow in the upper part of the body. Oscula were not appreciable, but pore sieves were identifiable in some fragments with ectosome. There is a 2 mm-thick, bristly ectosomal skeleton provided with spicules tufts (oxeas and cladotyles) that protrude 1–2 mm beyond the sponge surface. Spicules are oxeas, cladotyles, long-shafted dichotriaene, plesiasters, and amphiasters. Oxeas are curved, slender, slightly fusiform, in a wide size range (800 to more than 4000 × 20–55 μm); long fragments of isodiametric, 8 to 10 μm-thick oxeas also occur in the examined slides. Cladotyles are stout, nearly straight, somewhat fusiform, with a crown of 4 to 8 tubercles, and measuring 1200–2000 × 40–65 μm. Dichotriaenes with conical, slender rhabdomes (1500–3400 × 20–70 μm); protoclads and deuteroclads measuring 55–180 × 20–65 μm and 450–1100 × 20–60 μm, respectively. Plesiasters with 2 to 6, finely spiny actines, measuring 60–120 μm in total length. Amphiasters with finely spiny actines, measuring 10–22 μm in total length. The ectosomal skeleton consists of a feltwork of oxeas and cladotyles; it is also reinforced by amphiasters and the cladomes of the dichotriaenes. Oxeas and cladotyles form hispid tufts at the sponge surface, but also radial tracts that penetrate the choanosome along with the rhabdomes of dichotriaenes. Abundant plesiasters reinforce the internal pinacoderms.

Remarks. The type species is known from a single specimen collected from Balleny Islands (Antarctic shores) at 3000 m deep.

DERCITUS GRAY, 1867

Synonymy

[*Halina*] Bowerbank, 1858: 288 (preocc.). *Dercitus* Gray, 1867a: 542. *Battersbyia* Bowerbank, 1874b: 343.

Type species

Halina bucklandi Bowerbank, 1858: 288 (by subsequent designation; de Laubenfels, 1936a: 179).

Definition

Pachastrellidae with microscleres including toxas.

Diagnosis

Pachastrellidae having toxas as microscleres in addition to characteristic sanidasters with a thick central axis relative to the actines. Megascleres are calthrops or short-shafted triaenes; oxeas are absent.

Remarks

Halina Blainville, 1830: 497 predates [*Halina*] Bowerbank, 1858: 288 (according to Neave), with the former a junior synonym of *Halichondria* (see chapter on Halichondriidae). Consequently, although [*Halina*] Bowerbank, 1858 and *Dercitus* are objective synonyms (with the same type species), the former name is unavailable and the latter is here adopted. *Dercitus* is considered here to be a monotypic genus although it has been traditionally merged with *Stoeba* Sollas, 1888 – type species *Stoeba simplex* (Carter, 1880a) – following the concept of Topsent (1902) and Lendenfeld (1903). Following recommendations of Dendy (1905), Burton (1926), Vacelet & Vasseur (1971) and Maldonado (1993), and given that *Halina bucklandi* has toxas while *Stoeba* does not, the two genera are retained as distinct for the time being. The presence of toxas is of no value in providing information on the phylogenetic relationships of *Dercitus*, because no other astrophorid has them. A few toxa were described in the second record of the pachastrellid *Poecillastra rickettsi* de Laubenfels, 1930, but were subsequently regarded as being foreign (de Laubenfels 1932). Topsent's hypothesis (1902) that *Dercitus*' toxas are reduced euasters is unlikely because there is no remnant of a centrum. Conversely, vestiges of a centrum can be found in the reduced toxa-like asters of other astrophorids, such as *Erylus* (e.g., Topsent, 1927b; Pulitzer-Finali, 1983; Maldonado, 1992).

The microrhabdose form of the sanidasters, which has been the principal trait used to support the synonymy between *Dercitus* and *Stoeba* may be also deceiving when used to infer taxonomic relationships. The evolutionary paths through which the microrhabdose spicules of *Dercitus* (Fig. 9C) and *Stoeba* (Fig. 12B, D, E, H) have evolved (which are currently assumed to be sanidasters with reduced actines) are hard to retrace. It is probable that they have both evolved from a streptaster stage by actinal reduction. Nevertheless, we cannot rule out the hypothesis that they are derived from a microdiactinal stage, similar to the oval microstrongyles of *Pachastrella* or the small microxeas of *Characella*. Furthermore, reduced euasters, such as the ataxasters of some calthropellid genera (e.g., *Pachataxa* de Laubenfels, 1936a), have also converged to microrhabdose morphology (e.g., Topsent, 1897a; Lévi & Lévi, 1983a; Maldonado, 1993).

Description of type species

Dercitus bucklandi (Bowerbank, 1858) (Fig. 9).

Synonymy. *Halina bucklandi* Bowerbank, 1858: 288; 1861: 235; *Hymeniacidon bucklandi*, Bowerbank, 1866: 226; *Dercitus bucklandi*, Gray, 1868a: 542; *Pachastrella bucklandi*, Schmidt, 1870: 76; *Dercitus niger* Carter, 1871a: 3; *Battersbyia bucklandi*, Bowerbank, 1874b: 343.

Material examined. Holotype: Not seen. Slide of *Battersbyia bucklandi*: BMNH 1974, BK-542. Slide from Norman collection: BMNH 10.1.1.1705. Other material. Specimen of *D. bucklandi*; Burton: BMNH 1947.7.1.5a – Tombay Survey. Holotype of *Dercitus niger* Carter, 1871a : BMNH (no registration number found).

Description. Massive or cushion-shaped, sometimes filling cavities in hard substrata. Sponge surface is finely hispid. Oscules are 1–2 mm in diameter, isolated or in small groups, and with a distinctive sphincter-like structure. Ostioles are punctiform and irregularly scattered over the entire surface. The ectosome of the living sponge is black with gray or brown tinges, while the choanosome is beige to cream. Spicules are calthrops to short-shafted plagiotriaenes, sanidasters and toxa. Calthrops and short-shafted plagiotriaenes have clads measuring 170–450 × 30–50 μm; clads are often blunt, and incipiently divided in some of the plagiotriaenes. Sanidasters measure 27–35 × 2–6 μm and have a relatively thick, straight or curved central axis entirely covered by abundant minute actines, which make the spicule to look like a spiny microstrongyle. Toxa measure 50–110 × 1–1.5 μm, being slender and isodiametric, with pointed, smooth ends. The skeleton consists of a feltwork of sanidasters, the internal side of which is reinforced by the cladomes of short-shafted plagiotriaenes. The choanosomal skeleton consists of great abundance of calthrops and toxa, with scarce sanidasters.

Remarks. The type species occurs typically in sublittoral habitats of the northeastern Atlantic and the western Mediterranean (Templado *et al*., 1986), growing preferably in sites with low exposure to sun light.

PACHASTRELLA SCHMIDT, 1868

Synonymy

Pachastrella Schmidt, 1868: 64.

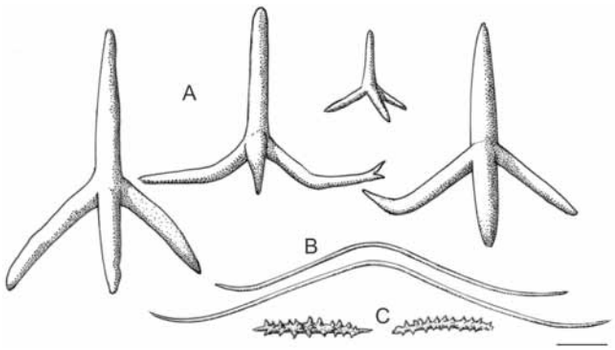

Fig. 9. *Dercitus. D. bucklandi*, holotype. A, calthrops (scale 175 μm). B, toxa (scale 10 μm). C, sanidasters (scale 10 μm).

Type species

Pachastrella monilifera Schmidt, 1868: 64 (by monotypy).

Definition

Pachastrellidae with microscleres including oval microstrongyles, but never microxeas. Its tetraxons do not become desmas.

Diagnosis

Pachastrellidae having oxea megascleres in one or more categories along with calthrops and/or short-shafted triaenes that can be mesotriaenes. Microscleres consist of oval microstrongyles that make an ectosomal feltwork and one or several kinds of streptasters that may include forms with reduced actines; they never are microxeas.

Remarks

It is worth noting that, unlike in the related genus *Brachiaster,* mesocalthrops never become tetracrepidal desmas.

After re-examining diverse material, it is concluded that several species originally described in *Pachastrella* belong to other genera, and vice versa. The holotype of *P. stylifera* Lendenfeld, 1897d (BMNH 27.III.MC3) and *P. tenuipilosa* Lendenfeld, 1906 (BMNH no registration number) are actually conspecific with *Poecillastra compressa*. The holotype of *P. amygdaloides* Carter, 1876 (BMNH 00047; I.1.2) also belongs to *Poecillastra* cf. *compressa*. *Pachastrella connectens* Schmidt, 1870 (BMNH I.1.1; 70.5.3.4.5) and *P. stellettodes* Carter, 1885e (BMNH I.1.I.1) are two valid species of *Characella. Pachastrella lesinensis* Lendenfeld, 1894 (BMNH 96.11.5.32–34) and *P. exostitus* Schmidt, 1868 (BMNH 08.9.24.80) are two valid species of *Stoeba* (Fig. 12C–H). The holotype of *Yodomia perfecta* Dendy, 1916c (BMNH MC5; RN.I to RN IX) and subsequent material collected by Burton (1956; BMNH 1936.3.4. 184) are conspecific with *Pachastrella ovisternata* (Fig. 10Q–N).

Description of type species

Pachastrella monilifer Schmidt, 1868: 15 (Figs 1D, 1R, 2D, 2H, 10A–N, 15R, 16D).

Synonymy. *Pachastrella abyssi* Schmidt 1870: 64; *Pachastrella caliculata* Kirkpatrick, 1902: 227; *Pachastrella isorrhopa* Kirkpatrick, 1902: 228.

Material examined. Holotype (fragment): BMNH 10.1.1.854 – Algeria. Slides of holotype: BMNH 1868.3.3.2. Holotype of *Pachastrella abyssi* Schmidt, 1870: BMNH 00036; 1870.5.3.59 (slides) – Florida. Other material. Slides of *P. abyssi*; Sollas, 1888: BMNH (no registration number) – South Atlantic. Slides of *P. abyssi*; Carter, 1876: BMNH Norman Coll. 10.1.1. 702–704: Cape St. Vincent. Slides of *P. monilifera*; Kirkpatrick, 1902: BMNH 24.5.1.74–75 – South Africa. Specimens of *P. monilifera*: BMNH 1936.3.4.144, 148, 149, 180 and 493 – Indian Ocean, John Murray Expedition. BMNH 33.8.12.12ba, 131;132; 33.8.13.133; 1947.2.15.3 – Siboga Expedition. BMNH 28.2.14.24 to 26 – 'Discovery' Expedition. Specimens of *P. monilifera*; Maldonado, 1993: CEAB-ALB-7–10a, -13, -18, -30, -32 and -35 – western Mediterranean. Holotype of *Pachastrella isorrhopa* Kirkpatrick, 1902: BMNH 02.2.13.4 to 6 – Natal Coast. Holotype of *Pachastrella caliculata* Kirkpatrick, 1902: BMNH 02.2.13.18 – South Africa. Specimens of *P. caliculata*; Lendenfeld, 1906: BMNH 08.2.9.107 to 110 – South Africa. Specimens of *P. monilifera*; de Laubenfels, 1935b: BMNH (no registration number) – Baja California. Holotype of *Pachastrella chuni* Lendenfeld, 1906: BMNH 08.2.9.111 to 114 – Cape Verde.

Description. Encrusting, massive or cup-like sponges, with a rough surface to the touch, the holotype being an irregular nodular fragment. Ostioles are punctiform, widely scattered through the body, sometimes grouped in small depressions of the surface. Oscules are irregularly scattered in most specimens, but concentrated on the internal side in cup-like forms, and over the lateral sides and the top of massive individuals. Oscules are 0.5 to 2 mm in diameter and may be fringed in white in alive specimens. Spicules are oxeas, calthrops, microstrongyles, and several types of streptasters. There are two categories of oxeas: 1) large, robust fusiform oxeas (950–1900 μm × 18–30 μm) similar to the choanosomal oxeas of other pachastrellids and (2) small, curved hastate oxeas (150–350 μm × 5–6 μm) similar to those found in the haplosclerid genus *Haliclona*. Calthrops occur in a large size variety, having conical, straight or curved clads that measure 150–800 μm × 8–100 μm and show occasional malformations. Microstrongyles are typically oval, microspiny, and slightly centrotylote spicules (8.5–15 μm × 4–6 μm). Small variations in microstrongyle morphology include oval and curved forms (Figs 2D, 10F), depending upon specimens. There are also elongated, spiny worm-like spicules (25–50 μm × 2–3 μm) that have been occasionally regarded to be microstrongyle-derived. Nevertheless, SEM observations (Fig. 2E) revealed that they are spiraster-like streptasters with a spiral shaft and reduced actines (Maldonado, 1993). Apart from these microrhabdose streptasters, typical amphiasters transitional to metasters occur, showing a 11–14 μm-long, relatively thick axis and short actines. The ectosomal skeleton consists of a feltwork of microstrongyles, irregularly reinforced by calthrops. The choanosomal skeleton is made of oxeas and calthrops scattered in high density and with no preferential arrangement through the body; oxeas never protrude the ectosome. Streptasters occur reinforcing the internal side of the ectosomal skeleton and the endopinacoderms.

Remarks. The type species occurs throughout the Atlantic and western Mediterranean, in sublittoral and bathyal depths growing on hard substrata in rocky and soft-bottom communities and caves (Pouliquen, 1972; Bibiloni, 1990). There are also records of the species from the Pacific (de Laubenfels, 1935b), the Antarctic (e.g., Koltun, 1964b), the Indian Ocean (Burton, 1959a), and the China Sea (Lévi & Lévi, 1989). However, a global revision of material should be undertaken before concluding that *P. monilifera* is a single cosmopolitan species. For example, some of the Indian ocean material revised here was found to belong to the related species *P. ovisternata*.

Some authors have regarded *P. monilifera* as a species with a variable spiculation, with dichotriaenes and mesodichotriaenes occasionally occurring in addition to calthrops (e.g., Topsent, 1902, 1904b). Nevertheless, a great deal of this reported variability is artificial and a consequence of lumping *P. ovisternata* into synonymy with *P. monilifera*. Indeed, *P. ovisternata* is a valid species characterized by the presence of long isodiametric, hispidating oxeas in addition to the typical, robust, fusiform choanosomal oxeas, as well as by the presence of dichotriaenes and

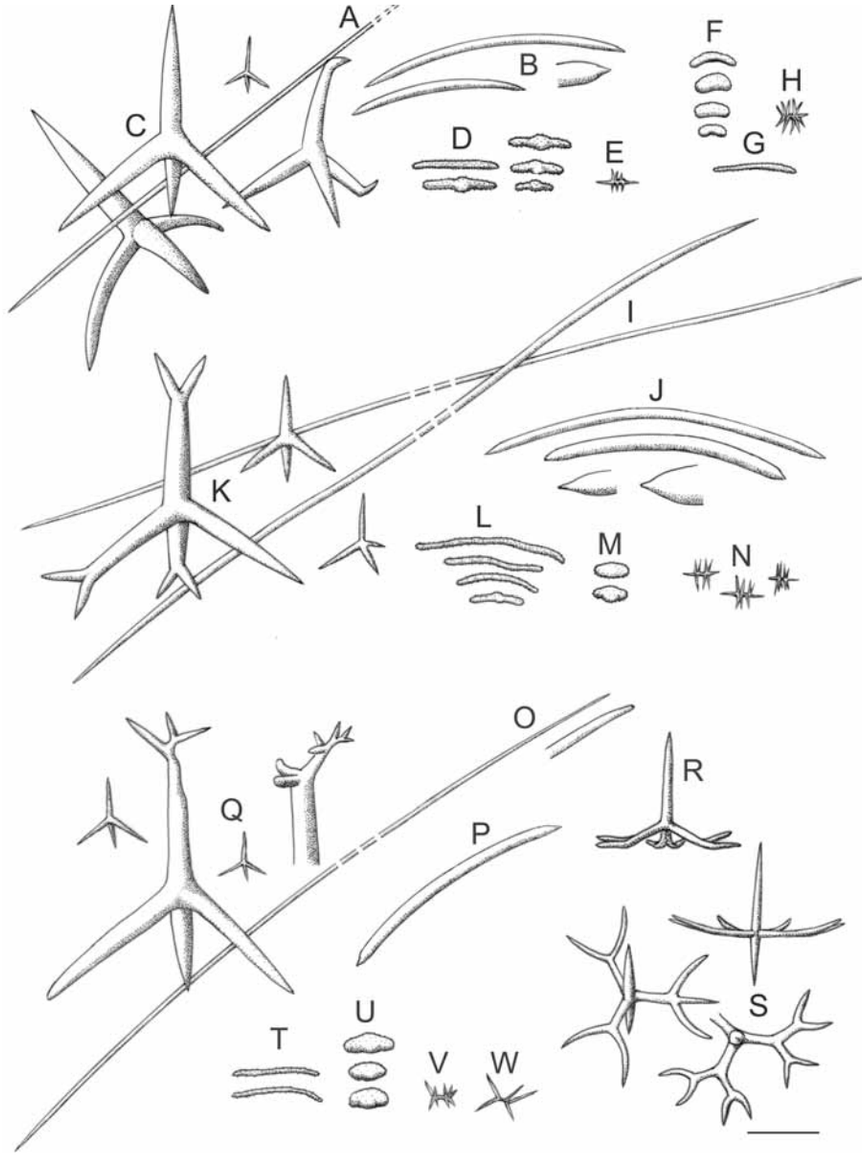

Fig. 10. *Pachastrella*. A–N, *P. monilifera*, holotype. A, fragment of oxea (scale 250 μm). B, hastate oxeas and detail of their end (scale 75 μm). C, calthrops (scale 250 μm). D, oval and lengthened microstrongyles (scale 25 μm). E, amphiaster (scale 25 μm). F–H, curved oval microstrongyles, spiraster-like microstrongyles, and a sanidaster (from Indo-Pacific specimens collected by Burton, 1959a) (scale 25 μm). I–N, oxeas, hastate oxeas, calthrops, spiraster-like microstrongyles, oval microstrongyles, and metaster-amphiasters (from holotype of *P. abyssi* (now *P. monilifera*)) (scales: I, 250 μm, J, 50 μm, K, 250 μm, L–N, 25 μm). O–W, *Pachastrella ovisternata*, from material formerly described as *P. abyssi* by Carter. O, oxea and detail of oxea end (scale 250 μm). P, hastate oxea (scale 75 μm). Q, calthrops and detail of malformation (scale 250 μm). R, dichotriaene (scale 150 μm). S, mesotriaenes (scale 150 μm). T, spiraster-like microstrongyles (scale 25 μm). U, oval microstrongyles (scale 25 μm). V, amphiaster (scale 25 μm). W, plesiaster (scale 25 μm).

mesodichotriaenes in addition to calthrops (Maldonado, 1993). Re-examination of material revealed that several BMNH specimens catalogued under diverse names belong to *P. ovisternata*: Norman collection from Cape St. Vincent (Fig. 10Q–W) labeled as *P. abyssi* O.S. by Carter (1O.1.1. 1702–1704); Stephens's (1915a) material from the Irish coasts labeled as *P. monilifera* (S.R. 151: 1953. 11.11.24); material from Madeira (1954.29.12); diverse material from the Indian ocean, such as the holotype of *Yodomia perfecta* Dendy, 1916c, and specimens of *Y. perfecta* and *P. monilifera* (Fig. 10F–H) collected by Burton (1959a). Mesotriaenes also occur in an undescribed *Pachastrella* from the Galapagos Islands (Fig. 1F–G).

In the material re-examined here there are nominal species, such as *P. abyssi*, *P. caliculata*, and *P. isorrhopa*, that are junior synonyms of *P. monilifera*. The presence of small dichotriaenes but no mesotriaene in the holotype of *P. chuni* from Madeira suggests that this may be a valid species, although close to *P. monilifera*.

The hastate oxeas described here in *P. monilifera* (Figs 1R, 10B, J) have traditionally been regarded as exogenous spicules. However, they have been found in the choanosome of all material of *P. monilifera* examined, including specimens originally described under different names. Similar hastate oxeas also occur in individuals of the close species *P. ovisternata* (Fig. 6P) as well

as in the closely related genus *Brachiaster* (Fig. 6B), and consequently these oxeas are considered to be characteristic of both genera.

POECILLASTRA SOLLAS, 1888

Synonymy

[*Normania*] Bowerbank, 1869a: 328 (preocc.). *Poecillastra* Sollas, 1888: 105. *Nethea* Sollas, 1888: 103. *Chelotropaena* Lendenfeld, 1906: 231.

Type species

Poecillastra compressa (Bowerbank, 1866: 55) (by original designation).

Definition

Pachastrellidae, the microscleres of which include always streptasters in the form of spirasters and plesiasters, as well as microxeas in a single category.

Diagnosis

Pachastrellidae whose megascleres are calthrops and/or short-shafted triaenes scattered through the whole choanosome. Microscleres consist of microxeas, always in a single size category, and several streptaster types, always including small spirasters and large plesiasters (transitional to metasters or amphiasters) with scarce, long actines.

Remarks

[*Normania*] Bowerbank, 1869a: 328 is preoccupied by *Normania* Brady, 1866, Crustacea, and therefore *Poecillastra* is the next available name. Re-examination of diverse museum collections discovered several species of *Poecillastra* that were originally assigned to other genera, and vice versa. The holotype of *Chelotropaena tenuirhabda* Lendenfeld, 1906 (BMNH 02.2.9. 104–106), from the Magellan Strait, appears to be a valid species of *Poecillastra* with short-shafted plagio- and dichotriaenes (Fig. 11G–N). *Stelleta scabra* Schmidt, 1868 (Fig. 11O–R; BMNH 68.3.2.41) from Algeria and *Pachastrella tenuipilosa* Lendenfeld, 1906 (BMNH no registration number) from the Central Atlantic are conspecific with *Poecillastra compressa* (Bowerbank, 1866). It is also worth mentioning that the skeleton of the holotype of *Sphinctrella theneides* Burton, 1959a (BMNH 1936.3.4.313a to 314a) looks very similar to that of *Poecillastra*, despite the fact that the sponge is subspherical, with a single osculum on the top and a single areolated, depressed area on the underside, both fringed by long, hispidating spicules, as typically found in *Vulcanella*.

Description of type species

Poecillastra compressa (Bowerbank, 1866) (Figs 2I, 11A–F).

Synonymy. *Ecionemia compressa* Bowerbank, 1866: 55; *Stelleta scabra* Schmidt, 1868: 19; *Hymeniacidon placentula* Bowerbank, 1874b: 189; *Normania crassa* Bowerbank, 1874b: 258; *Normania crassiuscula* Sollas, 1886a: 185; *Poecillastra incrustans* Sollas, 1888: 105; *Pachastrella stylifera* Lendenfeld, 1897d: 82; *Pachastrella tenuipilosa* Lendenfeld, 1906: 234.

Material examined. Holotype: BMNH BK.353, BK.354 – slides from *Ecinonemia compressa* Bowerbank, 1866. Holotype of *Normania crassa* Bowerbank, 1874b: BMNH BK-831 to 832; R.1631, R.1635. Specimens of *Ecionemia compressa*: BMNH 10.1.1.1686, 10.1.1.1688 – Norman coll., Shetland. Specimens of *Normania compressa*: BMNH 10.1.1.1129 to 1131 – Norman coll., Norway. Specimens of *Hymeniacidon placentula*: BMNH 10.1.1.1684 – Norman coll., Shetland. Specimens of *P. compressa*: BMNH 1887.9.30.8 – NE Atlantic, coll. H.M.S. 'Triton'. BMNH (no registration number) – Icelandic Ingolf Exp. Specimens of Stephens, 1915a: BMNH R.S. 483, 1953.11.11.19. Specimens of *P. compressa*; Maldonado, 1992: CEAB-ALB-6–5, ALB-6–22, ALB-7–21b – Mediterranean, Alboran Sea. Holotype of *Poecillastra incrustans* Sollas, 1888: BMNH 94.11.16.134 to 135 – North Atlantic. Holotype of *Pachastrella tenuipilosa* Lendenfeld 1906: BMNH (no registration number) – Central Atlantic. Holotype of *Stelleta scabra* Schmidt, 1868: BMNH 68.3.2.41 – Algeria.

Description. Polymorphous sponge often showing a plate-like (as the holotype) or cup-like body form, with punctiform ostioles distributed on one side of the sponge and 1–3 mm oscules usually provided with a contractile diaphragm and placed on the opposite sponge side. More rarely, the species is encrusting or massive. Alive specimens are whitish or pale yellowish. The spicules of the holotype consist of oxeas, calthrops and short-shafted orthotriaenes, microxeas in a single size category, large plesiasters transitional to amphiasters, and spirasters. Oxeas are fusiform, curved in the middle, with sharp ends, measuring 960–2080 × 15–35 μm. Calthrops and short-shafted orthotriaenes are relatively scarce, with actines measuring 125–400 × 10–20 μm. Tetraxons are frequently malformed and one or more actines can be missing in many spicules; the rhabdome is typically missing in those spicules that reinforce the ectosome. Microxeas are finely spiny, slightly curved, sometimes centrotylote, usually measuring 125–200 × 3–5 μm. Plesiasters transitional to amphiasters have three to five long actines relative to the central shaft; they are 35–55 μm in their greater diameter, with actines measuring 12–15 × 1 μm. Spirasters have a relatively thin axis of several revolutions and numerous, relatively large actines, measuring15–25 μm in total length. The ectosomal skeleton consists of a layer of tangential microxeas and streptasters. It is internally reinforced by calthrops, and bundles of oxeas that emerge from the choanosome and become brushes just under the ectosome. Oxeas very rarely hispidate the sponge surface. Microxeas and streptasters also occur in the choanosome, with streptasters preferentially reinforcing the endopinacoderms.

Remarks. The type species occurs in the northeastern Atlantic and the western Mediterranean over a wide depth range that goes from intertidal habitats (Sarà, 1964b) to depths of 3500 m (Koltun, 1970).

It has been suggested several times (e.g., Topsent, 1894d; Burton, 1930c) that the Indo-Pacific *P. laminaris* (Sollas, 1886a) (BMNH 94.11.16.120–130), the Southern Ocean *P. schulzii* Sollas, 1886a (BMNH 27.MC4, no number), and the Japanese *P. tenuilaminaris* Sollas, 1886a (BMNH 27.MC4, no number) are conspecific with the Atlantic-Mediterranean *P. compressa.* Re-examination of the respective holotypes confirmed that *P schulzii* is a valid species. Unlike *P. compressa*, it possesses two categories of oxea

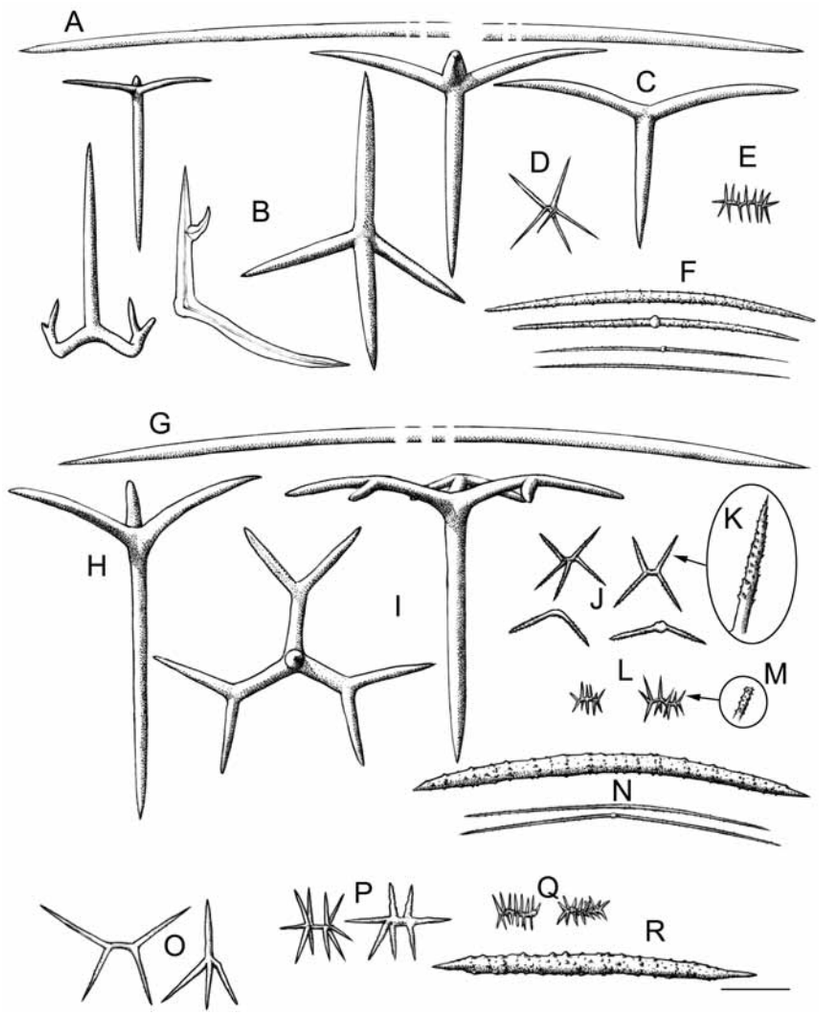

Fig. 11. *Poecillastra*. A–F, *P. compressa*, holotype. A, oxea (scale 125 μm). B, calthrop, short-shafted plagiotriaene and some malformations (scale 125 μm). C, triactinal calthrop tangential to the ectosome (scale 125 μm). D, plesiaster (scale 25 μm). E, spiraster (scale 25 μm). F, microxeas (scale 40 μm). G–N, *P. tenuirhabda*. G, oxea (scale 250 μm). H, short-shafted plagiotriaene (scale 250 μm). I, short-shafted dichotriaene (scale 250 μm). J, diactinal, tetractinal and pentactinal plesiasters (scale 40 μm). K, detail of plesiaster actine (scale 10 μm). L, spirasters (scale 40 μm). M, detail of spiraster actine (scale 10 μm). N, mature and thinner, developing microxeas (scale 50 μm). O–R, Microscleres of *Stelleta scabra* (now *Poecillastra compressa*), holotype. O, plesiasters (scale 20 μm). P, plesiasters transitional to amphiasters (scale 20 μm). Q, spirasters (scale 20 μm). R, microxea (scale 20 μm).

megascleres: fusiform, robust, choanosomal oxea and isodiametric, slender ectosomal oxeas that hispidate the sponge surface. *Poecillastra laminaris* from the Indo-Pacific is possibly a junior synonym of *P. schulzii*, as well as *P. eccentrica* Dendy & Burton, 1926 (BMNH R.N.V.I. 26.10.1.95) from the same area. In contrast, *P. tenuilaminaris*, which lacks the slender ectosomal oxeas, is probably a valid species. It resembles *P. compressa* in its skeleton but its plesiasters are transitional to metasters and are much smaller (only up to 22 μm in largest diameter). Diverse material from the Pacific coast of North America all appear to be conspecific with *P. tenuilaminaris,* including material of *P. tenuilaminaris,* de Laubenfels (1932) and Dickinson (1945), the holotype of *Poecillastra rickettsi* de Laubenfels, 1930 and subsequent Californian specimens (BMNH 19.8.22.7a, 29.8.22.7a) described by de Laubenfels (1932), which are contaminated with *Vulcanella* spicules. Thus, *P. schulzii* and *P. tenuilaminaris* should be regarded as valid species, the former occurring in the Indo-Pacific and the Southern Ocean and the latter occurring in the North Pacific from the Japan Sea to the American coasts.

STOEBA SOLLAS, 1888

Synonymy

Stoeba Sollas, 1888: 102. *Calcabrina* Sollas, 1888: 280. *Dercitancorina* Topsent, 1902: 13. *Halinastra* de Laubenfels, 1936a: 179. [*Dercitus* pars]

Type species

Samus simplex Carter, 1880a: 60 (by original designation).

Definition

Pachastrellidae having as microscleres only one or more categories of peculiar microrhabd-like sanidasters characterized by a relatively thick axis and reduced actines.

Diagnosis

Pachastrellidae in which the only megascleres, in most cases, are calthrops or short-shafted dichotriaenes; oxea megascleres are absent in most species but are present in two. Microscleres are sanidasters with a relatively thick axis and reduced actines, resembling spiny microrhabds. All known species are encrusting and often filling cavities in calcareous substrata.

Remarks

Sollas (1888) proposed *Stoeba* for *Samus simplex* Carter, 1880a from the Gulf of Manaar, but Lendenfeld (1903) followed by Topsent (1904b) and most modern authors merged it in *Dercitus*, whose type species possesses toxa. Following Dendy (1905), it is preferred here to retain the distinction between these two taxa for species with or without toxas given that the evolutionary origin of toxas within the order Astrophorida remains enigmatic and intriguing.

Apart from the type species, other apparently valid species of the genus are *S. plicatus* (Schmidt, 1868) from the Mediterranean (BMNH I.2.4), *S. occultus* (Hentschel, 1909) from Shark Bay, Western Australia, *S. extensa* Dendy, 1905 from Mutwal Island, Sri Lanka (BMNH 07.2.1.5a; 338.4.7a), *S. natalensis* Burton, 1926 from South Africa, and *S. syrmatitus* (de Laubenfels, 1930) from California (BMNH 1. 21). In addition, *Pachastrella lesinensis* Lendenfeld, 1894 from the Adriatic (BMNH 96.11.5.32–34), which is characterized by having oxeas, calthrop-like tetraxons and sanidasters with rounded ends, is also a valid species of *Stoeba* (Fig. 12F–H). Although its sanidasters were interpreted as microstrongyles by Lendenfeld, they are not like those in *Pachastrella* but are irregular and slightly twisted. *Pachastrella lesinensis* Lendenfeld is also the type species of *Dercitancorina* Topsent (1902: 13) (by original designation), which makes *Dercitancorina* a junior synonym of *Stoeba*. Apart from *S. lesinensis*, monaxonic megascleres are only known from material described as *Stoeba* spp Vacelet & Vasseur, 1971, in which thin strongyloxeas along with calthrops and sanidasters were found. *Pachastrella exostitus* Schmidt, 1868 from the Red Sea (BMNH 08.9.24.80), characterized by calthrops, thick sanidasters and tiny spheraster-like spicules with reduced actines is also a valid species of *Stoeba* (Fig. 12C–E). SEM observations have revealed that the spheraster-like spicules are slightly elongated, thus being a kind of compressed sanidasters or ataxasters (Fig. 2F–G). Consequently, because *Pachastrella exostitus* Schmidt, 1868 was also designated the type species of *Halinastra* de Laubenfels, 1936a, this latter genus becomes now a junior synonym of *Stoeba.* It is also concluded here that *Stoeba loricatus* (Lebwhol, 1914) is not a valid species, its holotype (BMNH 1942.6.12.11) being conspecific with *Pachastrella* c.f. *monilifera*.'

Description of type species

Stoeba simplex (Carter, 1880a) (Fig. 12A–B).

Synonymy. *Samus simplex* Carter, 1880a: 60; *Dercitus simplex*, Thiele, 1900: 20.

Material examined. Specimen of *Dercitus plicatus* var. *simplex* (Carter): BMNH (Ind. Mus. Coll. 31.1.1.21a) – Indian Ocean, Adaman Sea, Invisible Bank.

Description. Encrusting sponge, filling excavated cavities in calcareous structures. The skeleton consists of two spicule types, short-shafted dichotriaenes and sanidasters. Dichotriaenes with protoclads being clearly shorter than deuteroclads. In BMNH specimens, protoclads are 30–50 × 12–60 μm and deuteroclads are up to 150 × 35–40 μm; rhabdome is 40–225 × 60–75 μm, and 210 × 42 μm in the holotype. Sanidasters have a thick, slightly twisted axis and reduced actines, measuring 22–28 × 4–6 μm in total length. The sanidasters are extremely abundant in the ectosome, making a feltwork that is reinforced at their inner side by the cladome of the triaenes; the rhabdomes point inwards.

Remarks. The type species is known from the Indian Ocean (Gulf of Manaar, Adaman Sea), excavating Melobesian nodules and other calcareous structures, from uncertain depth.

THENEA GRAY, 1867

Synonymy

Thenea Gray, 1867a: 541. *Tisiphonia* Thomson, 1869a: 712. *Dorvillia* Kent, 1870c: 293. *Wyvillethomsonia* Wright, 1870: 80. [*Dorvilia*] Poctâ, 1883: 382 (*lapsus*). *Clavellomorpha* Hansen, 1885: 19. *Thisiphonia* Lendenfeld, 1887b: 563. *Theuca* Lundbeck, 1907: 559.

Type species

Tethea muricata Bowerbank, 1858: 308 (by original designation).

Definition

Pachastrellidae with specialized poriferous areas and root-like processes for attachment to the substratum, which are partially made of flexuous anatriaenes. Its microscleres always include streptasters in the form of plesiasters; microxeas are absent.

Diagnosis

Distinctive ovate or mushroom-shaped sponges, with radial or bilateral symmetry, with one to few oscula at upper portion of the body, and with at least part of the ostia grouped in a one or more inhalant areas located near the equator of the body, in a transversal recess. Because most species live in deep, soft bottoms, the sponges are provided with basal, root-like processes for anchoring to the sediment or buried substrata. The transversal recess, sometimes provided with a protruding palisade of spicules, is thought to prevent the inhalant areas from clogging by the fine silt that characterizes deep-sea habitats (Fig. 3A–C). The skeleton consists of at least a type of monaxons (oxeas and/or oxeotylotes), one or more types of long-shafted tetraxons (dichotriaenes, anatriaenes, mesoanatrienes, protriaenes, mesoprotriaenes, and/or orthotriaenes), and one or more categories of streptasters (plesiasters, amphiasters, metasters, spirasters); true microxeas are always absent, although plesiasters reduced to two-ray, microxea-like forms may occur in some species.

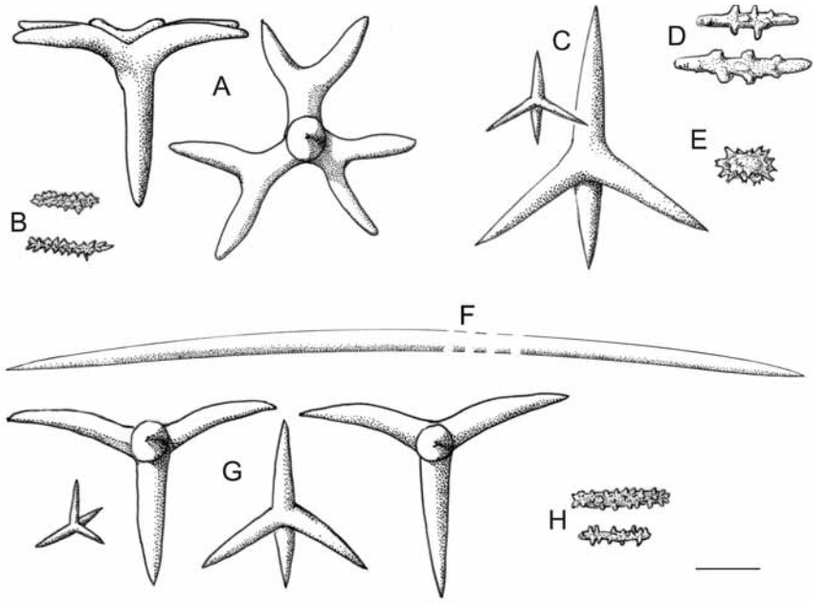

Fig. 12. *Stoeba*. A-B, *S. simplex*. A, dichotriaenes (scale 100 μm). B, sanidasters (scale 25 μm). C–E, *S. exostitus*, holotype. C, calthrops (scale 100 μm). D, sanidasters (scale 15 μm). E, ataxaster (scale 15 μm). F–H, *S. lesinensis*, holotype. F, oxea (scale 150 μm). G, calthrops (scale 100 μm). H, sanidasters (scale 15 μm).

Remarks

Owing to the large size that the plesiasters attain in some species (e.g., *T. novazelandiae* Bergquist, 1961c) they have occasionally been misinterpreted as megascleres and described as spiny calthrops. However, true calthrops have never been found in *Thenea*.

Description of type species

Thenea muricata (Bowerbank, 1858) (Figs 1A, 3A–C, 13).

Synonymy. *Tethea muricata* Bowerbank, 1858: 308; *Thenea muricata*, Gray 1867a: 541; *Wyvillethomsonia wallichii* Wright, 1870: 8; *Dorvillia agariciformis* Kent, 1870c: 293; *Tisiphonia agariciformis*, Thomson, 1873: 167; *Clavellomorpha minima* Hansen, 1885: 19; *Thenea schmidtii* Sollas, 1886a: 183; *Thenea intermedia* Sollas, 1888: 97.

Material examined. Holotype: BMNH I.1.7. Other material. Specimens of *Thenea muricata*: CEAB collections – Gibraltar Straits (Maldonado, unpublished). Comparative material. BMNH types of *T. delicata* Sollas, 1886a, *T. megastrella* Lendenfeld, 1903, and *T. grayi* Sollas, 1886a; Sollas's (1888) material of *T. fenestrata* (Schmidt, 1880b), ZIL material of *T. delicata* Koltun (1964b).

Description. Ovate to mushroom-shaped sponges, 0.5 to 2 cm in diameter, white to gray in color. Giant individuals – up to 12 cm in diameter – have been described from the Norwegian fjords (Steenstrup & Tendal, 1982). One or few open oscules (2–5 mm in diameter) placed at the upper part of the body. One or more areolated areas located within a transversal recess that may also be provided with a protruding palisade of megascleres. This spicule palisade may form a complete rim at the equator of the sponge body, occur at some points only, or, more rarely, be absent, depending upon individuals. Most individuals develop a variable number of flexible root-like processes made of naked, entangled spicules that allow the anchoring of sponges in soft bottoms. At the upper part of the body, budding processes for asexual reproduction may occur. The skeleton consists of oxeas, dichotriaenes, protriaenes and anatriaenes as megascleres; microscleres are plesiasters and spirasters. Oxeas are isodiametric, curved or flexuous, measuring in the holotype 2000–5000 × 10–15 μm, but up to 15 mm in giant individuals. Dichotriaenes have conical, long, somewhat flexuous rhabdomes, measuring up to 5000–6000 × 150 μm; protoclads are shorter than deuteroclads, measuring 100–330 × 30–100 μm and 300–1100 × 30–80 μm, respectively. Protriaenes have a straight rhabdome measuring up to 5000 × 30 μm, and curved or straight clads measuring 150–400 × 12–20 μm. Anatriaenes have thin, flexuous rhabdomes measuring up to 300 × 25 μm, and straight, conical clads measuring 40–140 × 15–20 μm. The form of the asters is affected by some inter-individual variability; in the holotype, the plesiasters have 2 to 6, finely spiny, 40–100 μm long actines. The spirasters, which measures 25–35 μm in total length, occur in two morphologies: (1) with relatively few, long actines and a thin central shaft; (2) with many short actines and a relatively thick, central shaft. The latter category occurs exclusively at the ectosome of the inhalant areas. The skeletal arrangement follows a clearly radial pattern. The oxeas, along with the rhabdomes of the tetraxons, form fascicles that penetrate radially from the sponge surface to the innermost choanosome. The oxeas also protrude beyond the sponge surface, giving support to the budding processes for asexual reproduction and forming the hispid, equatorial palisade that protects the inhalant areas. The cladomes of the tetraxons, along with the spirasters, reinforce the ectosome, and may protrude the sponge surface here and there. Spirasters and plesiasters occur everywhere in the body, the former being more abundant in the ectosome and the latter ones in the endosome. The rootlet processes are mainly made by entangled anatriaenes.

Remarks. The abundant literature on this species indicates that *T. muricata* shows a significant intraspecific variability in external morphology, dimensions and abundance of the various spicule types (Boury-Esnault *et al*., 1994b). The type species occurs in the northeastern Atlantic and the Mediterranean, mostly in deep waters (120–4020 m depth) and preferably in soft-bottom

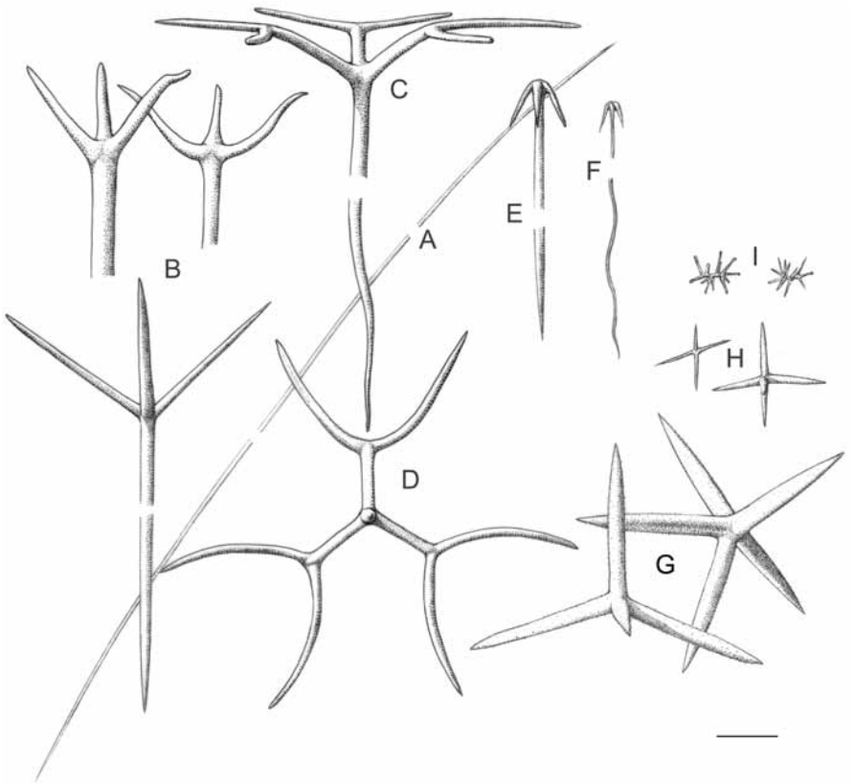

Fig. 13. *Thenea. T. muricata*, holotype. A, oxea (scale 300 μm). B, protriaenes (scale 150 μm). C–D, dichotriaenes (scale 250 μm). E, choanosomal anatriaene (scale 150 μm). F, anatriaene from the root-like processes (scale 150 μm). G–H, plesiasters in a wide size range (scale 50 μm). I, spirasters (scale 50 μm).

communities. There are also records of the species in sublittoral caves (Russ & Rützler, 1959; Sarà, 1964b; Rützler, 1966).

TRIPTOLEMMA DE LAUBENFELS, 1955

Synonymy

[*Triptolemus*] Sollas, 1888: 93 (preocc.). *Triptolemma* de Laubenfels, 1955b: E43.

Type species

Triptolemma cladosus (Sollas, 1888: 93) (by original designation).

Definition

Cryptic Pachastrellidae having megascleres exclusively short-shafted mesotriaenes with diversely branched clads, but never becoming mesotrider desmas.

Diagnosis

Pachastrellidae that penetrates the tissue (parasitises?) of other sponges. It is characterized by megascleres that are exclusively short-shafted mesotriaenes with diversely branched clads. Microscleres are streptasters in one or two categories, with microxeas occurring in some species.

Remarks

There are four known species in the genus: *T. intextus* (Carter, 1876) from Cape St. Vincent, northeastern Atlantic (Fig. 14B–E; BMNH 10.1.1. 1693–97), growing on and in *Corallistes bowerbankii*; *T. incertus* (Kirkpatrick, 1903a), from South Africa (Figs 1H–I, 2C, 14F–I; BMNH 02.5.2b–5b), growing on and in *Discodermia natalensis*; *T. simplex* (Sarà, 1959a), from the Mediterranean, growing within various demosponges; *T. cladosus* (Sollas, 1888) from Ki Island, Indian Ocean. This latter species possibly also occurs in the Gulf of Manaar (Carter, 1880a), where it has been regarded as an Indian population of the North-Atlantic *Samus parasiticus* Carter, 1876. Indeed the holotype of *S. parasiticus* from Cape St. Vincent appears to be conspecific with *T. intextus* and was proposed by Lévi & Lévi (1983a) to be a junior synonym of *T. intextus*.

Monaxonic megascleres are absent in all species, since, according to Sarà (1959a), those reported in the literature of *T. cladosus* and *T. intextus* (Fig. 14B) presumably belonged to the host sponges.

Description of type species

Triptolemma cladosus (Sollas, 1888) (Fig. 14A).

Synonymy. *Samus quadripartita* Carter (unpublished manuscript).

Material examined. Three slides containing also spicules of the host sponge *Corallistes thomasi* (BMNH 1891.5.4.12) were examined, but only a few microscleres potentially belonging to the

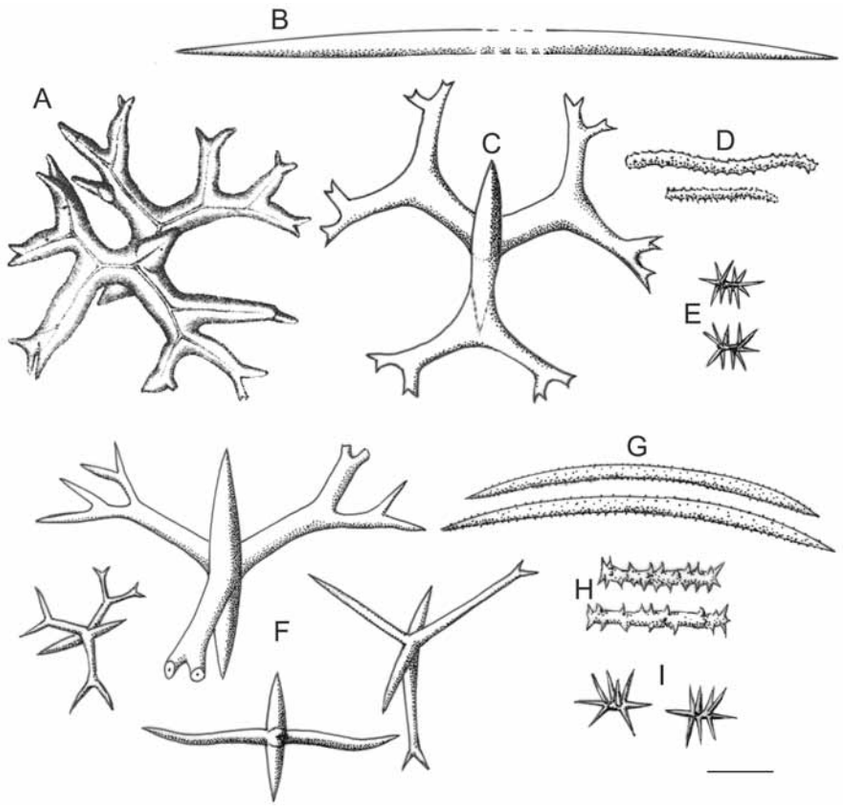

Fig. 14. *Triptolemma*. A, *T. cladosus*, holotype, mesotriaene with irregular, tetrafurcated clads (redrawn from Sollas, 1888) (scale 35 μm). B–E, *T. intexta*, holotype (redrawn from Carter, 1876). B, oxeas, the exogenous nature of which has been suggested (scale 50 μm). C, short-shafted mesotriaene with tetrafurcate clads (scale 50 μm). D, sanidasters (scale 10 μm). E, metasters transitional to amphiasters; note that microxeas occur, but are not illustrated (scale 10 μm). F–I, *T. incertus*. F, short-shafted mesotriaenes with diversely branched clads (scale 100 μm). G, spiny microxeas (scale 20 μm). H, sanidasters (scale 10 μm). I, metasters (scale 10 μm).

holotype of *T. cladosus* were found. No other type material appears to be available. Therefore, the holotype description below follows Sollas (1888: 93).

Description. Encrusting specimen growing on and penetrating the tissue of a *Corallistes*. The skeleton consists of short-shafted mesotriaenes, microxeas and sanidasters (formerly described as trichose microxeas) and spirasters. Mesotriaenes have symmetrical, short and blunt rhabdomes that measure up to 60 × 21 μm each; clads are irregularly trifurcated or tetrafurcated, with desmoid appearance. The dichotomy of the cladome is not confined to a single plane and the level of division also varies within a spicule, co-occurring dichotomous and tetrafurcated clads; protoclads are up to 52 × 21 μm, deuteroclads up to 55 μm long, tritoclads up to 27.6 μm long, and tetraclads up to 27.6 μm long. Microxeas were formerly described as being smooth – although this is unsupported by the current knowledge on other species in the genus – and more or less fusiform, measuring up to 118 × 4 μm. Sanidasters have a relatively thin axis covered with minute, erect spines and measure up to 27.6 μm in total length. Spirasters have a thin axis provided with relatively long and thin actines and measure up to11.8 μm in total length. The skeletal arrangement consists of abundant sanidasters forming an ectosomal feltwork in which the cladomes of the mesotriaenes are embedded tangentially to the sponge surface.

Remarks. Sollas (1888) was unsure about whether oxea that he observed belonged to *Triptolemma* or to its host *Corallistes*. Although the issue remains unsolved, Sarà (1959a) pointed that most evidence suggests that all four known species of *Triptolemma* lack oxeas.

VULCANELLA SOLLAS, 1886

Synonymy

[*Sphinctrella*] Schmidt, 1870: 65 (preocc.). *Vulcanella* Sollas, 1886a: 186. *Sphincterella* de Laubenfels, 1936a: 180.

Type species

Vulcanella horrida (Schmidt, 1870: 65) (by original designation).

Definition

Pachastrellidae with special cribriporal oscula surrounded by a palisade of protruding oxeas (Fig 3D–E) and with one or more microsclere types showing an annulate decoration (Fig. 2B).

Diagnosis

Encrusting, thick lamellate or submassive Pachastrellidae in which oscula are grouped in specialized exhalant areas – called

'fenestrate cloacas' sensu Sollas (1888) – and fringed by a protruding palisade of flexuous, atrial oxeas. Oxeas are in two categories, slender atrial oxeas and stout choanosomal oxeas. Tetraxonic megascleres are absent in some species (subgenus *Annulastrella* n. subg.), but calthrops transitional to short-shafted triaenes, occasionally dichotriaenes, are present in most species (nominal subgenus *Vulcanella*). Microscleres consist of one or two categories of microxeas, which may be absent in some species, and one to several types of streptasters. Streptasters are usually metasters and spirasters (Fig. 2K), more rarely amphiasters; triactinal and calthrop-like plesiasters with annulate actines also occur in the subgenus *Vulcanella*.

Remarks

Some species of *Vulcanella* have small both calthrop-like and triactinal spicules. These microscleres have been misinterpreted by some authors, who regarded them as true megascleres, called microtriods and microcalthrops. However, accumulation of observations over time has made it clear that the number of actines in these spicules may range from 2 to 6, depending on the species. This indicates that they are derived from asters, possibly plesiasters with an extremely short central axis. Similarly, the large plesiasters with four actines that occur in some species of *Thenea* have occasionally been misinterpreted as true megascleres. It is interesting that asters converging on calthrop-like morphologies also occur in other unrelated sponge lines, such as, for instance, in the hadromerids *Timea cumana* and *T. tetractis* (e.g., Maldonado, 1992).

In most species of *Vulcanella*, one or more types of microscleres (i.e., the largest microxeas and plesiasters) show an annulate ornamentation which originates from the coalescence of microspines to make verticils or spires (Fig. 2B). This ringed ornamentation may be a useful and reliable diagnostic tool at the generic level, although there are some species where this feature can only be seen under SEM (e.g., *V. cribrifera*, *V. aberrans, V. cribiporosa*). Furthermore, there are many species described prior to the use of SEM techniques for which we have no data on ringed ornamentation, requiring comprehensive re-examination using new techniques to assess the utility of spiny verticils in microxeas and/or streptasters as a diagnostic trait.

In an attempt to organise the skeletal variability in *Vulcanella*, two subgenera are proposed here. Nominal subgenus *Vulcanella* is erected for *Vulcanella* species that always have tetraxonic megascleres and microxeas, but lack triactinal and tetractinal plesiasters with annulate actines. *Annulastrella* subgen. nov. is created for those species that lack tetraxonic megascleres, but possess triactinal and calthrop-like plesiasters with annulate actines, with or without microxeas as microscleres.

VULCANELLA (*ANNULASTRELLA*) SUBGEN.NOV.

Type species

Vulcanella (Annulastrella) annulata (Carter, 1880a: 140) (by monotypy).

Synonymy

Tisiphonia annulata Carter, 1880a: 140; *Sphinctrella annulata*, Sollas 1888: 100.

Definition

Vulcanella lacking tetraxonic megascleres and possessing large plesiasters with two to six annulate actines.

Diagnosis

Vulcanella lacking tetraxonic megascleres. Oxeas may be either absent or present in one or two categories (atrial and choanosomal oxeas), depending on species. Microscleres are large plesiasters with two to six annulate actines (traditionally called microtriods and microcalthrops), along with one or two categories of smaller streptasters (spirasters, metasters or amphiasters). Although annulate microxeas have been described in some species, it is likely that they are plesiasters reduced to a diactinal stage in most cases, except those described by Topsent (1923) in material of *Stellettinopsis annulata* Schmidt, 1880b.

Remarks

Apart from the type, three species are included in this subgenus. *Sphinctrella verrucolosa* Pulitzer-Finali, 1983, from the western Mediterranean, is characterized by atrial and choanosomal oxeas, spirasters (ranging to metasters and amphiasters), annulate plesiasters with 2–6 actines, and a category of annulate, centrotylote microxeas, which probably are plesiasters reduced to a diactinal stage. *Sphinctrella ornatus* Sollas, 1888 (Sollas, 1888; Topsent, 1892a, 1904b, 1928c) from the Azores and Cape Verde (north-eastern Atlantic Ocean), is characterized by atrial and choanosomal oxeas, spirasters, metasters (to amphiasters), and annulate plesiasters, the number of actines of which varies from 2–5. *Stellettinopsis annulata* Schmidt, 1880b, from the Gulf of Mexico, is characterized by atrial and choanosomal oxeas, spirasters, metasters, plesiasters with three to four finely annulate actines, and spiny, non-annulate microxeas (Topsent, 1923). Note that *Stellettinopsis annulata* Schmidt, when transferred to the genus *Vulcanella* (*Annulastrella*), becomes a junior secondary homonym of the type species *Vulcanella* (*Annulastrella*) *annulata* Carter, and is renamed here as *Vulcanella (Annulastrella) schmidti* nom. nov., after its former author.

Topsent (1923, 1928c) considered the species mentioned above, excluding the recently described *V. verrucolosa*, to be junior synonyms of *V. annulata* (Carter). However, small differences in their skeletons and the enormous geographical distance between populations make it sensible to maintain the Mediterranean, the Indian, the north-eastern and north-western Atlantic material as separate species.

Triassic and Cretaceous species of the genus *Monilites* Carter, 1871b are apparently related to *Vulcanella*, as they have similar, annulate microxeas and plesiasters (see Wiedenmayer, 1994). In my opinion, no relationship can be supported between the annulate microscleres of *Vulcanella* and the cricostyles and ringed protriaenes found in Jurassic-Cretaceous deposits (see Wiedenmayer, 1994).

Description of type species

Vulcanella (Annulastrella) annulata (Carter, 1880a) (Fig. 15).

Synonymy. *Tisiphonia annulata* Carter, 1880a: 140.

Material examined. None. The description is taken from Carter (1880a) from specimens dredged up from the Gulf of Manaar (Indian Ocean).

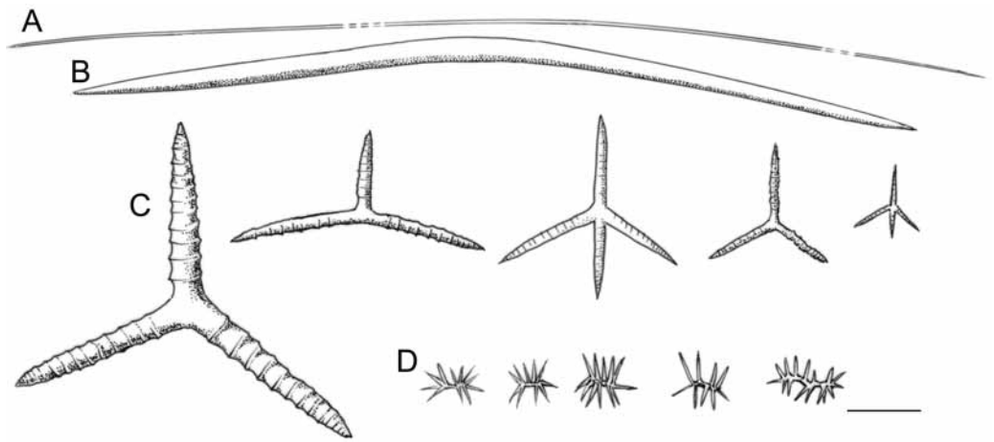

Fig. 15. *Vulcanella (Annulastrella). V. (A.) ornata*, holotype. A, cloacal oxea (scale 250 μm). B, choanosomal oxea (scale 250 μm). C, triactinal and tetractinal, annulate, plesiasters (scale 50 μm). D, spirasters (scale 30 μm). Spicules illustrated are very similar to those of the type species, *V. (A.) annulatus*, see Carter (1880a).

Description. Massive, white sponge measuring 2.12 mm in diameter and growing among the detritus attached to a large, massive specimen of another astrophorid sponge (from Carter, 1880a). The megascleres consist of fusiform, slightly curved, oxeas measuring 885 × 20 μm. The microscleres consist of four-rayed plesiasters, the actines of which measure up to 240 × 20 μm and are covered by minute microspines arranged in marked rings; there are also spirasters with a relatively thin axis and numerous long actines, measuring above 12.7 μm in total length.

Remarks. The type species is known from the Indian Ocean (Gulf of Manaar and Ambon; Carter, 1880a; Topsent, 1897a; Desqueyroux-Faundez, 1981)

VULCANELLA (VULCANELLA) SOLLAS, 1886

Type species

Vulcanella (*Vulcanella*) *horrida* (Schmidt, 1870): 65.

Definition

Vulcanella species that have tetraxonic megascleres and microxeas but lack triactinal and tetractinal plesiasters with annulate actines.

Diagnosis

Nominative subgenus containing *Vulcanella* species that have tetraxonic megascleres and microxeas but lack triactinal and tetractinal plesiasters with annulate actines. Microxeas are spiny, with spines arranged in either a marked annulate pattern or a nearly uniform distribution, depending upon species.

Description of type species

Vulcanella (*Vulcanella*) *horrida* (Schmidt, 1870) (Fig. 16B–F).

Synonymy. *Sphinctrella horrida* Schmidt, 1870: 65.

Material examined. Holotype (slide): BMNH-70.5.3.4a – containing only a piece of peripheral choanosome and the ectosome that covers an osculum remains as the only extant type material for this species. BMNH BK 1251, BK 1252a–f – slides from two specimens labeled as *S. horrida* by Bowerbank. Comparative material. Holotype of *Sphinctrella horrida* Schmidt, 1870: BMNH 70.5.3.47. BK12524a–f, BK1251 – material from America and Florida labeled by Bowerbank. Holotype of *Sphinctrella gracilis* Sollas, 1888: BMNH 94.11.16.144–146 (slides) – Cape Verde. MSNG NIS.70.2, PF.455, CEAB-ALB-7–11cx – Mediterranean specimens described by Pulitzer-Finali (1983) and Maldonado (1993), respectively. Syntypes of *Sphinctrella aberrans* Maldonado & Uriz, 1996a: CEAB-POR.BIO 173a–c – Alboran Sea. Specimens of *Vulcanella tricornis* (Wilson, 1904): HBOI, unpublished – Galapagos Islands. Holotype of *Sphinctrella cribrifera* Sollas, 1886a: BMNH 89.1.1.39 – Cape Verde. MSNG PF-268: – Mediterranean specimens erroneously reported by Pulitzer-Finali (1983) as *S. horrida*. Holotype of *Sphinctrella theneides* Burton, 1959a: BMNH 1936.3.4.313a-314a – Maldives Island. Holotype of *Sphictrella ornatus* Sollas, 1888: BMNH 94.11.16.146–149 – Cape Verde. BMNH SR.353, 1953.II.II.27 – material described Stephens (1915a) from Irish waters.

Description. A 2–3 cm thick plate, with rounded edges, rough surface, and oval elongated atriums lined by a fenestrated membrane and fringed by a palisade of long spicules (Sollas, 1888). The skeleton consists of atrial and choanosomal oxeas, calthrops, microxeas in two categories, and spirasters. Only a broken, 12 μm-thick, atrial oxea occurs in the type slide, but fusiform, slightly curved choanosomal oxeas are up to 3000 × 85 μm; oxeas measuring up to 5000 × 142 μm were reported in a redescription of the type (Sollas, 1888). Calthrops are mostly well-formed, with clads measuring 400–1100 × 40–100 μm. Microxeas in the large category are fusiform, stout, with a very patent ringed ornamentation, and measure 200–500 × 8–13 μm. Microxeas in the small category measure 100–180 × 3–4.5 μm, being comparatively slender, finely spiny, and with a ringed pattern only perceptible around the middle of the spicule. Spirasters are 12–18 μm in length, with numerous, short actines and a relatively thick axis with two or three revolutions.

Remarks. The type species is recorded from the North Atlantic, from Florida (e.g., Schmidt, 1870; unpublished material labeled by Bowerbank in BMNH) to the Azores (e.g., Topsent,

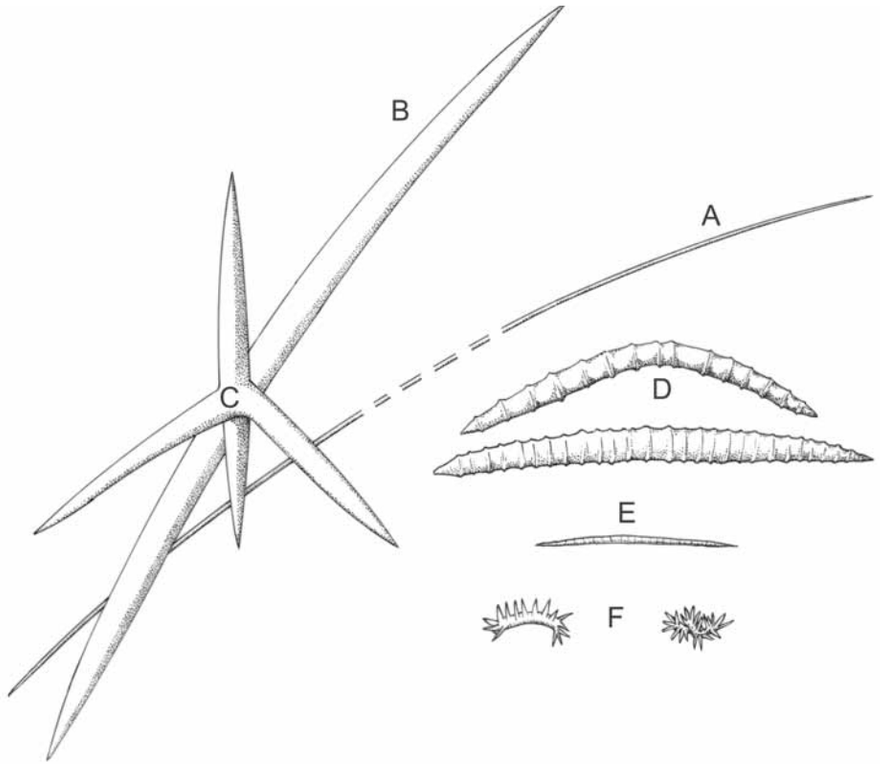

Fig. 16. *Vulcanella (Vulcanella). V. (V.) horrida*, holotype. A, atrial oxea (scale 300 μm). B, choanosomal oxea (scale 300 μm). C, caltrop (scale 200 μm). D, large, annulate microxeas (scale 50 μm). E, small, uniformly spiny microxeas (scale 50 μm). F, spirasters (scale 15 μm).

1904b, 1928c), at depths of 60–2500 m. It has erroneously been reported in the Mediterranean (Pulitzer-Finali, 1983) as result of a misidentification of fragmentary material probably belonging to *Vulcanella cribrifera* (see Maldonado & Uriz, 1996a).

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